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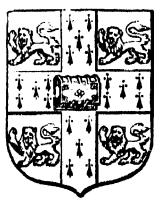
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A. G. TANSLEY

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WITH THIRTY-EIGHT PLATES, AND NUMEROUS FIGURES
IN THE TEXT



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CORRECTION

Journal of Ecology, XVI, 1.

p. 187, line 30, for *Gymnostomum donianum* read *Grimmia doniana*.

PRINCIPLES OF CLASSIFICATION OF THE SPRUCE
COMMUNITIES OF EUROPEAN RUSSIABY V. N. SUKACHEV¹.*(With one Figure in the Text.)*

The spruce is the most characteristic tree of the forests of the northern half of European Russia; therefore the forest or taiga zone is called the spruce zone.

Within the limits of European Russia the northern limit of the area of this tree passes through the northern part of the Kola Peninsula, not reaching, by the way, the limit of tree vegetation. In the Kola Peninsula typical *Picea excelsa* Linn. (European spruce) already does not occur. The forms approach *Picea obovata* Ldb. (Siberian spruce), and to the east of the White Sea the northern limit of spruce is represented by this latter species alone.

The southern limit of the spruce coincides in European Russia exactly enough with the northern limit of the chernozëm. Beginning from the central part of the province Volhynia, the limit of the spruce runs north of the province Kiev, through the province Bryansk, the western part of the province Tula and the southern part of the province Nizhni-Novgorod, forming a large tongue along the River Sura. Then the limit again rises north of the Volga, which it crosses near Kazan and runs towards the Kama, along which it takes a north-eastern direction, crossing the Kama in the southern part of the province Perm and proceeding eastward as far as the Ural, along which it descends to 53½° of N. lat. But here it passes over into *P. obovata* Ldb.

Thus the spruce occupies one-half the area of European Russia but its distribution is not uniform. Proceeding southward, it becomes thinner and its dominance is shared by pine and oak. In the more northerly provinces spruce is the most widely spread species. East of the Ural Mountains it is not easy to distinguish the areas of European and Siberian spruce, because over a large area these two species present a series of intermediate forms. If, then, we take the two together, it can be said that in the northern provinces, including those of the north-west, the spruce occupies on the average 44 per cent. of the forest area. But a considerable part of the area occupied by deciduous trees, partly by the pine, and also the part now under tillage, were, before the introduction of culture by man, doubtless covered by the spruce; and we may say that in the primitive covering of the whole north of Russia the spruce forests prevailed (dominated) and occupied the greater part of the territory.

¹ The author's name (with the rest of the Russian names in this paper) is spelt in accordance with the recommendations of the British Academy's Committee on the transliteration of Russian names into English. The author, however, desires it to be understood that he is better known outside his own country by the German form of his name—"Sukatschew."—EDIT., *Journal of Ecology*.

In the last few decades many botanists, and foresters in particular, have dealt with the investigation of spruce forests¹. But the descriptions of the different types of spruce community have been so brief that it is impossible to compare them accurately or to give them a satisfactory classification. Below an attempt is made to arrive at the basis of such a classification.

In order to elucidate the laws of distribution of the spruce communities, it is necessary first to characterise, if only briefly, the geo-morphological features of the regions in which they occur.

The greater part of the spruce region of European Russia is, on the whole, a plain, except towards the Ural, the Timan range and the peninsula of Kola, and most of it consists of sandy and loamy glacial and fresh water deposits. Only in the region of the northern marine transgression do we find marine deposits. In a few places rocks, including limestones (which are sometimes dolomitised), reach the surface. Omitting the rock outcrops, we have, for the spruce region of European Russia, particularly the northern part, the following geo-morphological schema. In a sufficiently developed river valley beyond the low banks which are subject to inundation, and occupied by meadows, comes a terrace, partly sandy, which is followed by the true bank. The areas between the rivers nearest to the river valleys are usually drained by them and also by their tributary gorges, the valleys of brooks, etc.; at a distance from the river valleys we meet, on the contrary, with less drained and often more level areas, which are thus more liable to become moory. The good forests, therefore, not infrequently border the rivers in broader or narrower bands, while further away from the rivers an inferior forest is sometimes succeeded by extensive high-moors. This fundamental regularity in the distribution of forests is typical in the northern part of the spruce region not only of European Russia but also of West Siberia.

Hence we are able to trace the following five typical habitats of spruce forest: (1) more or less nutritive clayey loam or sandy loam soils, well drained in places with sufficiently pronounced relief, in the north for the most part adjoining the rivers, (2) similar soils but becoming already moory, with worse drainage, less developed relief, in the north for the most part situated farther from the rivers, (3) soils still more moory, without differentiated relief, level, situated still farther from the rivers. These three types of habitat form, as it were, a connected series. Besides these there are (4) the bottoms of narrow valleys where there is excessive moisture, but the water is for the most part in motion, and (5) places carrying (for the north) exceptionally rich soils, most often connected with neighbouring limestone rocks.

According to these five fundamental habitats of the spruce we can divide the spruce forest into five types which differ in the phytosociological structure of their communities, as well as in the size of the trees. A

¹ These papers having been all published only in Russian, I did not think it requisite to annex any list of them.

conspicuous character is the presence and composition of the lower strata of the community. ³

Therefore the following scheme of classification for spruce associations may be given:

1. Relief adequately developed; site well drained, soils more or less nutritive, loams, clays or sandy loams, not moory—**Piceeta hylocomiosa**.

2. Relief less developed, sites feebly drained, soils the same, but already somewhat moory—**Piceeta polytrichosa**.

3. Relief undeveloped, surface flat, site not drained, soils moory—**Piceeta sphagnosa**.

4. Bottom of depressions with moory soils, but running water—**Piceeta herbosa**.

5. Sites with nutritive well-drained soils, for the most part in the neighbourhood of limestone deposits—**Piceeta fruticosa**.

Each of these types is composed of a series of plant communities. Owing to insufficient investigation full species lists of these communities cannot yet be given.

1. PICEETA HYLOCOMIOSA.

These are characterised by the first layer consisting of spruce only (in the north-east not seldom with admixture of fir), sometimes also with soft wood deciduous trees (aspen and birch), absence of a special second layer, absence of any marked shrub stratum, a grass stratum which is neither dense nor abundant but consists of characteristic species, and a strong continuous stratum of mosses (*Pleurozium schreberi*, *Hylocomium proliferum*, *Dicranum undulatum* and others). On the whole, the *Piceeta hylocomiosa* occupy the poorer and fresh or moist soils. Within these limits there is, however, a certain variety of soils. In some cases they may be simply sand, in others loam, in others, again, a drier sandy loam. The spruce, being a plant of marked sociological dominance, grows successfully on these various soils, and levels the other conditions to such a degree, that it creates on all the soils communities of very similar character.

The second tree stratum is usually wanting. The shrub stratum is either completely absent or represented by rare shrubs of *Sorbus aucuparia*, and, less frequently, *Lonicera xylosteum*, *Rhamnus frangula*, *Daphne mezereum* and, in the north, *Rosa acicularis*. In places which have preserved their primitive character to a high degree, these shrubs are feebly developed, owing to the deep overshadowing of the soil. *Lonicera xylosteum* and *Daphne mezereum* stand the overshadowing better than the other shrubs.

The herb stratum is usually not continuous and is poor in species, developing in patches consisting sometimes of one species, sometimes of a mixture of several. The following is a list of plants most characteristic of the herb stratum of this group of communities. In this list the degree of the *exclusiveness* or

fidelity (*Fidélité*, *Gesellschaftstreue*) of each species is added, according to the system of J. Braun-Blanquet and J. Pavillard, where the number 5 indicates the strictest connection of the given species to this group of associations: a similar estimation is given to the plants according to the *constancy* or persistence with which they are found in the *Piceeta hylocomiosa*. These notes are given on the basis of the conception of these plants drawn from the study of the literature on the spruce forests of the north and personal acquaintance with these forests.

| | Exclu- siveness (Fidelity) | Constancy (Per- sistence) | | Exclu- siveness (Fidelity) | Constancy (Per- sistence) |
|----------------------------------|----------------------------------|---------------------------------|------------------------------|----------------------------------|---------------------------------|
| <i>Phegopteris polypodioides</i> | 5 | 3 | <i>Hepatica triloba</i> | 4 | 3 |
| <i>Ph. dryopteris</i> | 4 | 4 | <i>Anemone nemorosa</i> | 4 | 5 |
| <i>Polystichum spinulosum</i> | 3 | 4 | <i>Oxalis acetosella</i> | 4 | 5 |
| <i>Lycopodium annotinum</i> | 3 | 3 | <i>Rubus saxatilis</i> | 3 | 3 |
| <i>L. selago</i> | 5 | 1 | <i>Fragaria vesca</i> | 2 | 5 |
| <i>Poa nemoralis</i> | 2 | 3 | <i>Circaea alpina</i> | 5 | 4 |
| <i>Aira flexuosa</i> | 3 | 3 | <i>Pirola rotundifolia</i> | 3 | 4 |
| <i>Millium effusum</i> | 3 | 3 | <i>P. secunda</i> | 4 | 5 |
| <i>Luzula pilosa</i> | 3 | 5 | <i>P. media</i> | 3 | 3 |
| <i>Maianthemum bifolium</i> | 4 | 5 | <i>P. minor</i> | 3 | 2 |
| <i>Paris quadrifolia</i> | 3 | 4 | <i>P. uniflora</i> | 5 | 2 |
| <i>Convallaria majalis</i> | 3 | 3 | <i>Monotropa hypopitys</i> | 3 | 2 |
| <i>Epipogon aphyllus</i> | 5 | 1 | <i>Vaccinium vitis-idaea</i> | 2 | 5 |
| <i>Neottia nidus avis</i> | 3 | 1 | <i>V. myrtillus</i> | 3 | 5 |
| <i>Platanthera bifolia</i> | 3 | 3 | <i>Trientalis europaea</i> | 4 | 5 |
| <i>Gymnadenia cucullata</i> | 4 | 1 | <i>Melampyrum nemorosum</i> | 3 | 3 |
| <i>Goodyera repens</i> | 5 | 4 | <i>M. pratense</i> | 4 | 4 |
| <i>Corallorhiza innata</i> | 3 | 3 | <i>Veronica officinalis</i> | 3 | 3 |
| <i>Calypso bulbosa</i> | 5 | 1 | <i>Galium triflorum</i> | 5 | 2 |
| <i>Asarum europaeum</i> | 3 | 3 | <i>Linnaea borealis</i> | 5 | 4 |
| <i>Stellaria frieseana</i> | 4 | 3 | <i>Solidago virgaurea</i> | 3 | 5 |
| <i>Actaea spicata</i> | 3 | 3 | <i>Lactuca muralis</i> | 5 | 2 |

If the herb stratum of the *Piceeta hylocomiosa* has no considerable density, the moss stratum, on the contrary is usually quite continuous, consisting chiefly of *Hylocomium proliferum*, *Rhytidiadelphus triquetrus*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Dicranum undulatum*, *D. scoparium*, more rarely *Polytrichum commune*, *P. juniperinum*, *Rhodobryum roseum* and some species of *Sphagnum*.

This stratum usually covers the soil with a continuous soft thick carpet. Under the layer of living moss there is not seldom a rather thick dead covering (up to 5–8 cm.), consisting partly of the remains of Phanerogams, chiefly of dead debris of moss. In some cases it has the character of peat.

From all this we see that the *Piceeta* of this type is very consistent in its structure. In this case the spruce may be called, in the full meaning of the word, the *builder* (*édificateur*) of the association. It greatly influences the conditions of the habitat, the soil as well as the atmosphere under its canopy, and through them the composition of flora and the ecology of the other members of the adult association. Notwithstanding a certain general monotonousness of this type there may still be distinguished (from the composition of the herb and moss strata on the one hand, the character of the growth of the

spruce on the other, and partly from the participation, though a feeble one, of other species in the uppermost tree stratum) separate communities closely connected with the soil conditions, among which the first place must be assigned to the conditions of moistening and aeration of the soil connected with it, or more exactly, the conditions of penetration into the soil of oxygen, and the second place to the abundance or poverty of the soil in nutritive substances.

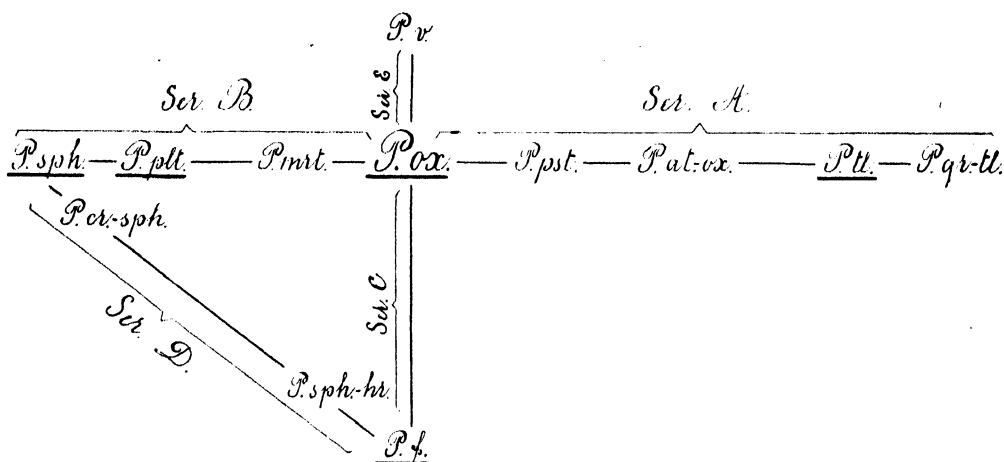


FIG. 1. Diagram of ecological series of spruce associations (*Piceeta*) of European Russia.

| | |
|---|--|
| <i>P.ox.</i> = <i>P. Piccotum oxalidosum</i> | <i>P.f.</i> = <i>P. fontinale</i> |
| <i>P.mrt.</i> = <i>P. myrtillosum</i> | <i>P.sph.-hr.</i> = <i>P. sphagnoso-herbosum</i> |
| <i>P.plt.</i> = <i>P. polytrichosum</i> | <i>P.pst.</i> = <i>P. polystichosum</i> |
| <i>P.sph.</i> = <i>P. sphagnosum</i> | <i>P.at.-ox.</i> = <i>P. atragenoso-oxalidosum</i> |
| <i>P.cr.-sph.</i> = <i>P. caricoso-sphagnosum</i> | <i>P.tl.</i> = <i>P. tiliosum</i> |
| <i>P.v.</i> = <i>P. vaccinosum</i> | <i>P.gr.-tl.</i> = <i>P. quercoso-tiliosum</i> |

Therefore the different communities belonging to this type may be characterised on the one hand by the process of growth and the volume at a certain age of the tree stratum and on the other by the character of the herb and moss strata, but only within the limits of a certain natural region. The communities characterised, for instance, by the prevalence of *Oxalis acetosella* will, under different physical conditions, differ in growth and volume as well as partly by a different secondary vegetation. In this case we may speak of the presence of definite geographical vicarious subassociations.

The chief associations belonging to this group are the following:

(a) *Piceetum oxalidosum*. Characteristic is the considerable participation in the herb stratum of *Oxalis acetosella*, *Maianthemum bifolium*, *Circaea alpina*, etc. It usually occupies the best, well-drained soils in the region covered with spruce. The tree stratum is high, well formed, and clear of branches to a great height. The second tree stratum and the shrub stratum are usually wanting, but sometimes there occur infrequent bushes of *Salix caprea*, *Lonicera xylosteum*, *Daphne mezereum*. Of mosses *Rhytiadelphus triquetrus* (*Hylocomium triquetrum*) is often dominant, but *Pleurozium* (*Hypnum*) *schreberi* is also

abundant; *Hylocomium proliferum* (*H. splendens*), *Rhodobryum roseum* and others are less frequent; here belongs the *Oxalis-Myrtillus* type of Cajander and other Finnish botanists.

(b) *Piceetum myrtillosum* is characterised by the prevalence in the field stratum of *Vaccinium myrtillus* and the absence or feeble distribution of *Oxalis acetosella* and other indicators of better soils. It occupies somewhat inferior and moister soils than the *P. oxalidosum*. The tree stratum is of lower growth and yields a smaller volume of timber. The second layer is absent. There is no shrub stratum, or only here and there *Sorbus aucuparia*, *Rhamnus rangula* and *Lonicera xylosteum*. The most frequent moss is *Hylocomium proliferum* (*H. splendens*), less frequent are *Pleurozium* (*Hypnum*) *schreberi*, *Ptilium crista-castrensis*, *Dicranum undulatum*, *D. scoparium*, *Polytrichum juniperinum* and *P. commune*. Here belongs the *Myrtillus* type of Cajander.

In its typical form this community is widely distributed in the more level areas of north and north-west of Russia.

(c) *Piceetum atragenoso-oxalidosum*. This is doubtless a distinct community represented by the type of the spruce-larch forest in the Orlovsk forest in the district Veliki-Ustyug, where above the spruce layer there towers a thin stand of immense larch trees. In the thin shrub stratum are *Tilia cordata*, *Lonicera xylosteum*, *Sorbus aucuparia* entwined by the creeper *Atragene sibirica*. In the herb stratum, together with indifferent spruce indicators, we have the indicators of rich soils: *Asarum europaeum*, *Oxalis acetosella* and others. In this case we have, properly speaking, one of the stages of the replacement of the larch by the spruce. The limits of the area of this community are unknown.

(d) *Piceetum polystichosum* is another distinct spruce community with a dense fern stratum. This occurs on good soils and is distinguished by good growth of the spruce. *Polystichum spinulosum* is especially characteristic. Up to the present time this association has been described only by Damberg for the forest district of Tikhvin in the district of Cherepovets.

(e) *Piceetum empetroso-vaccinosum*. An association often developed in the far north of the forest region occupying cool and even somewhat dry loamy and sandy loam soils. The first layer consists of spruce with an admixture of birch. The trees are low, of slow growth, hung with lichens; and there are great quantities of dead wood. The shrub stratum is thin, consisting of *Sorbus aucuparia* and low juniper. The herb stratum is composed of *Vaccinium vitis idaea*, *V. myrtillus*, *Empetrum nigrum*, *Aira flexuosa*, *Lycopodium complanatum*, and in some places *Cornus suecica*. The moss stratum is continuous, but not too thick, consisting of *Pleurozium schreberi*, *Ptilium crista-castrensis* with admixture of *Polytrichum commune* and lichens (*Cladonia* and others).

This community is essentially vicarious in the north with the two first described and is distinguished phytosociologically by a somewhat lesser influence of the spruce on the rest of the vegetation, since tree growth is here strongly depressed by the general unfavourable climatic conditions.

2. PICEETA POLYTRICHOSA.

This type is characterised by the first layer consisting of spruce more or less intermingled with birch. The second layer is entirely wanting. The shrub stratum is even less developed than in the preceding type. The growth too is much worse: the trees do not attain a large size, and are often hung with *Usnea barbata*. The herb stratum is considerably poorer in species and number of individuals. On the other hand, there is a very characteristic continuous carpet of *Polytrichum commune* into which the foot sinks. The communities belonging to this type occupy, as a rule, level, rather low lying, areas with podsol soil super-saturated with water.

Compared with the *Piceeta hylocomiosa*, the spruce as the creator and the builder of the community is somewhat weaker, since the massive stratum of *Polytrichum commune* in some degree reduces its rôle, taking part of it upon itself. Therefore, though the influence of the spruce on the environment is still great even here, it nevertheless does not attain its full force, and the inferior development of the tree canopy allows of the development of less shade-resistant forms, while the massive stratum of *Polytrichum* has an unfavourable influence on the natural regeneration of the spruce and on most of the representatives of the herb stratum peculiar to *Piceeta hylocomiosa*. The compact mass of *Polytrichum commune*, decomposing with difficulty, offers an important obstacle to the development of the superficial root system of the spruce and of horizontally growing rhizomes. If the preceding type of spruce forest was characterised by an unequal distribution of the herb stratum, growing in patches, and consisting of one or another species of herb, here, on the contrary, we have a more equal distribution of these plants, not showing a tendency to form large patches.

Particularly typical of the herb stratum is the considerable share taken by *Equisetum silvaticum*, which is a sign of the poor quality of the soil and of the excessive moisture. Further there is a luxuriant growth of *Vaccinium myrtillus*, while *Vaccinium vitis idaea*, though it does occur, obviously takes a second place. Not infrequent are *Orchis maculata*, *Corallorrhiza innata*, *Lycopodium annotinum*, *Melampyrum pratense* and *M. silvaticum*, *Linnaea borealis* (particularly on tussocks and elevations around stumps), sometimes the rare *Ledum palustre* and even *Rubus chamaemorus*.

Besides *Polytrichum commune* the moss carpet contains a larger or smaller amount of *Pleurozium schreberi*, *Hylocomium proliferum*, *Dicranum scoparium*, and more rarely an admixture of some species of *Sphagnum*.

The *Piceeta* of this type are rather monotonous and do not present such a variety of communities as the *Piceeta hylocomiosa*; they are widely distributed over the whole north of Russia. The two following may be distinguished:

(a) *Piceetum polytrichosum* to which applies everything said of the entire group. Here must also be referred the type "paksu-sammal-typpi" (thick moss type, Dickmosstyp, HMT of the Finns).

(b) *Piceetum empetroso-polytrichosum*. The forests of this community occupy large stretches in the far north of the forest region, particularly in the Pechora district. They occupy moist podsol soils. The uppermost tree layer consists of spruce with an admixture of birch; it is low, thin, of very bad growth. The second tree layer is wanting. The shrub stratum, owing to the first layer being thin, is more developed but nevertheless thin, consisting of *Salix bicolor*, *S. nigricans*, *S. caprea*, *Sorbus aucuparia*, *Juniperus communis* and *Rosa acicularis*. The herb stratum is more varied, consisting of a mixture of the representatives of the preceding community and *Empetrum nigrum*, *Ledum palustre*, *Rubus arcticus*, *R. humulifolius*, *Carex globularis* and, to some extent, of the representatives of the community *Piceetum myrtillosum*. The moss stratum is composed of *Polytrichum commune*, with *Sphagnum*, *Ptilium crist-i-castrensis*, *Cetraria islandica* and some other lichens.

In comparison with the preceding one this community is distinguished by the circumstance that both the "builders"—the spruce and *Polytrichum*—are strongly depressed by the unfavourable general climatic conditions and therefore their influence on the other elements is considerably less.

This community essentially succeeds the preceding one geographically, but is rather sharply separated from it.

3. PICEETA SPHAGNOSA.

The general features of the communities of this group are the very depressed growth of the spruce, which yields almost no building material, poor development of the tree canopy, the admixture, sometimes considerable, of birch, and sometimes of pine and black alder, a considerable participation in the moss stratum of *Sphagnum*, which sometimes supplants all other mosses. Soil very moist, often with a considerable peat horizon.

If in the preceding type the rôle of the spruce as "builder" of the association is disputed by *Polytrichum*, here the competitor, and a successful one, is *Sphagnum*. The spruce has already no considerable influence on the environment, it is rather itself under the control of the environment, which is in a considerable degree a creation of the sphagnum carpet. Therefore in the herb stratum the participation of the usual representatives of the spruce forest is reduced to a minimum; there are, on the contrary, predominating bog plants.

In dependence on the degree of bogginess, whether the water stagnates or is running, the thickness of the peat layer, the degree to which the water is mineralised, there arise different communities distinguished by the character of the growth of the spruce, as well as by the admixture of other species.

To this group there can be referred a considerable number of communities, which are however up to the present very inadequately described. As instances there may be mentioned two as examples:

(a) *Piceetum sphagnosum*. This community usually represents a stage of the conversion of *Piceetum polytrichosum* into bog. It occupies depressed,

for the most part level stretches, with stagnating or slowly running water and a more or less considerable layer of peat. As the process of conversion into bog proceeds and the sphagnum peat becomes thicker the spruce begins to be supplanted by the pine. The growth of the spruce is usually very depressed and the spruce itself is shortlived. The admixture of birch is usually inconsiderable. The second tree layer and the shrub layer are wanting; in the region farther to the north the dwarf birch (*Betula nana*) is frequent. In the herb stratum along with the species peculiar to *Piceeta polytrichosa*, such as *Equisetum silvaticum*, *Vaccinium myrtillus*, *V. vitis-idaea* (on the tussocks), *Orchis maculata*, there are already met with representatives of the sphagnum bog, such as *Ledum palustre*, *Vaccinium uliginosum*, *Rubus chamaemorus*, sometimes *Comarum palustre*, *Menyanthes trifoliata*. There are also not a few small sedges.

The moss stratum consists for the most part only of *Sphagnum*, sometimes with an admixture, chiefly on tussocks, of *Polytrichum* or *Pleurozium schreberi*.

In its typical form this association seems to be distributed chiefly in the north-west of Russia and partly in the north, without spreading to the north-east.

(b) *Piceetum caricoso-sphagnosum*. Boggy *Piceetum* with varied herb stratum in which, for the most part, species of *Carex* predominate. This association occupies low, level, basin-like sites, with a surface covered with tussocks, and holes filled with water between the tussocks. Water running slowly or stagnating. The tree stratum consisting of thin, low spruce, intermingled with birch and often pine. Shrub stratum thin; *Rhamnus frangula*, *Alnus incana*, *Ribes nigrum* occur the most frequently; in some places *Lonicera xylosteum* and others. Herb stratum varied, consisting of a mixture of the representatives of spruce forest on tussocks, and different bog plants, sedges, grasses, with sometimes *Phragmites communis*, often *Athyrium filix femina* and others. Moss stratum usually not continuous; on tussocks consisting of sphagnum, *Polytrichum commune*, and less frequently *Pleurozium schreberi*. This community has a rather wide distribution in the north, and is mostly called "sogra."

4. PICEETA HERBOSA.

Piceeta with dense, high herb stratum. The characteristic feature of this *piceetum* is its connection with the bottoms of the valleys of small rivers and brooks, forming narrow bands with nutritive, moist, even wet soil, flooded by spring freshets, but always with running water. The tree stratum is not dense and consists of spruce and birch. The shrub stratum is fairly well developed. The herb stratum is dense, high and luxuriant; the moss stratum on the contrary is feebly developed.

The representatives of this group of communities are:

(a) *Piceetum fontinale*. This community has a considerable distribution in the valleys of small rivers, brooks and springs, where between the trees, in

the open or covered by densely growing grass, more seldom by moss carpets, murmurs the cold running water. It is characterised by the following features (including the features of the whole group). The spruce reaches a great size, grows strongly, but not with well-formed trunks. The second tree stratum is wanting. The shrub stratum is developed rather strongly and consists of *Ribes nigrum*, *R. rubrum*, *Sorbus aucuparia*, *Prunus padus*, *Juniperus communis*, *Rosa acicularis*, *Lonicera coerulea*, *Tilia cordata*, *Viburnum opulus*, *Ulmus pedunculata*, and in the north-eastern part of the region also fir.

The herb stratum is vigorous, dense, high and rich in species. The following are characteristic: *Aconitum excelsum*, *Ulmaria palustris*, *Cirsium oleraceum*, *Angelica silvestris*, *Aegopodium podagraria*, *Comarum palustre*, *Calla palustris* and other species. On tussocks: *Vaccinium vitis-idaea*, *V. myrtillus*. The degree of development of the moss carpet varies considerably but it is as a rule insignificant. On tussocks there are found the usual mosses of spruce forests as well as *Polytrichum commune* and (rarely) *Sphagnum*.

(b) *Piceetum sphagnoso-herbosum*. This community is characterised by a much worse growth of the spruce, which seldom reaches normal size. The shrub stratum (mainly *Alnus incana*) is poor in species, and also the herb stratum which has fewer tall herbs (*Cirsium oleraceum* and *Aegopodium podagraria* entirely disappear). A great rôle is played by ferns and by the representatives of the usual spruce forest species. The moss stratum is thicker and a much greater part is played in it by *Sphagnum*. The appearance of this community is caused by diminished flow of the water, less enrichment of the soil by spring freshets and by somewhat poorer soils in general.

5. PICEETA FRUTICOSA.

This group is characterised by a good growth of the spruce and the participation of broad-leaved trees. These either enter into the uppermost layer or take part in the second layer only, or in the shrub stratum. Very characteristic is the dense and varied shrub stratum. The herb stratum is moderately developed, often with an admixture of species characteristic of broad-leaved forest. The moss carpet is mostly not thick and not continuous. The soils of these communities are fresh or even a little dry, and always fairly rich in nutritive salts.

These communities are characteristic of the southern part of the spruce region, where they are distributed rather widely.

The degree of participation in the community of other species of trees, as well as the development and composition of the shrub, herb and moss strata and the growth of the spruce itself depends on the greater or lesser fertility of the soil and its humidity. This forms the basis of distinction between the associations belonging to this group. Full lists, however, must wait for the future.

Instances are the following:

(a) *Piceetum tiliosum*. A piceetum with a *Tilia* stratum. In its region of distribution the lime, as a shade-resisting plant, sometimes occurs as an isolated shrub in the shrub stratum in *Piceeta hylocomiosa*. On better soils, however, *Tilia* forms a dense shrub stratum, into which enter a considerable number of other species of shrubs. In such cases the spruce usually makes good growth, but there is always some admixture of aspen and birch, also fir (in its region of distribution) as well as isolated pines. The second tree layer does not attain any perceptible development. In the shrub stratum besides *Tilia cordata*, there are *Euonymus verrucosus*, *Rhamnus frangula*, *Lonicera xylosteum*, *Corylus avellana*, *Daphne mezereum*, *Viburnum opulus* and other shrubs, the composition varying somewhat according to the region.

The herb stratum is of average or considerable density. Along with the usual representatives of spruce forest such as *Oxalis acetosella*, *Maianthemum bifolium*, *Linnaea borealis*, *Pirola rotundifolia*, *P. secunda*, *Trientalis europaea*, *Vaccinium myrtillus*, *Convallaria majalis*, *Goodyera repens*, we find *Asarum europaeum*, *Pulmonaria officinalis*, *Mercurialis perennis*, *Asperula odorata* and other species characteristic of broad-leaved forest. The moss stratum is feebly developed or altogether wanting; it consists mostly of *Rhytidiadelphus triquetrus*, *Dicranum undulatum*, *Pleurozium schreberi*.

Even within the limits of Central Russia and the southern parts of northern and north-eastern Russia this association varies considerably, and when studied in detail several subordinate communities will probably have to be distinguished. Of these attention may be called to the type described by Finnish botanists for southern Finland: "Käen-kaali-lehdet" (*Oxalis-Maianthemum* type, OMaT).

(b) *Piceetum quercoso-tiliosum*. Piceetum with oak and other broad-leaved species. This is connected with a further amelioration of the soil and at the same time a complication of the community. Usually it develops on the richest soils, often with underlying limestone and marl.

The spruce makes very rapid growth, attaining great height. Together with it in the same layer there are found oak, and often lime, maple, ash, elm; also pine, birch, aspen. In the region of distribution of fir the shrub stratum is rich, sometimes even richer than in the preceding communities, consisting of the same forms. Especially luxuriant development is often shown by *Euonymus verrucosus*.

In the herb stratum, which in its composition is near to that of the preceding group though usually thinner, there already predominate forms peculiar to broad-leaved forests supplanting the representatives of spruce forests. The moss stratum is either entirely wanting or feebly developed; it consists chiefly of *Rhodobryum roseum*.

This community is distinguished by considerable variability and after more detailed investigation will certainly have to be divided into a series of

distinct communities, among which there will be found such as succeed one another geographically. It is developed chiefly in the southern part of the forest region, nearer to the forest-steppe, seldom penetrating into the depth of the forest region in places where limestone exists close beneath the soil.

Being variable, as already mentioned, this community in some cases approaches the broad-leaved forest, where the oak and concomitant species begin to prevail; in other cases it approaches the preceding communities. The interference of man or injury to the spruce caused by bark-beetles is ready to alter the interrelation of the species of the coniferous and deciduous trees in this community, giving prevalence to the latter.

Considering the different communities formed by the spruce, we see that the *Piceeta hylocomiosa* represent communities, the interrelation of whose elements is particularly perfect. This type is the most persistent, and must be regarded as the most fundamental of the spruce communities, for not only has the dominant tree a great influence on the rest of the vegetation of the community which is very closely adapted to this influence, but the dominant itself is closely adapted to the conditions so brought about: for instance, the carpet of characteristic mosses is specially suited to the regeneration of the spruce from seed. The closeness of these interrelations of different parts of the community is the criterion of high social integration, and probably of long duration.

In this respect the first place among all the communities belonging to this group must be assigned to the *Piceetum oxalidosum* and the *P. myrtillosum*. These two, which are, on the whole, near each other morphologically, appear to be also genetically close. The development of phytosociological integration has proceeded in both during thousands of years. But nevertheless the *P. myrtillosum* is the starting point of a series of communities, which departing from *P. oxalidosum* and passing through *P. polytrichosum*, leads to the extermination of spruce forest, a series connected with the process of conversion of forest into bog, and terminating, so far as *Piceeta* are maintained, with the *P. sphagnosum*, which is, in its turn, followed by the succession to *Pinetum*, and the ultimate replacement of forest by bog.

This process, the succession accompanying the increasing bogginess of the soil, is observed in spruce forests where the soil is not enriched by springs or the freshets of small rivers and brooks which so abundantly water our northern forests. The most complex of these wet forests and at the same time those in which the growth of the spruce is best is the *Piceetum fontinale* (Russian *log*). The further development of this association has two possible courses. As the river develops its valley and the bed becomes deeper, the soil becomes better drained, and in the course of time the community may pass over to one of the group of *Piceeta hylocomiosa*. In the second case, where the drainage is bad and peaty deposits continue to accumulate, the feeding of the upper layers of soil by springs and floods decreases every year. This causes an impoverishment

of the herb stratum, an increased development of the mosses and a worse growth of the spruce, which result in the replacing of *Piceetum fontinale* by *P. sphagnoso-herbosum* (*sogra*), whose natural course of development again leads in the course of time to sphagnum bog with stunted crooked pine. Thus in this second case we have a series of successions analogous with that mentioned above (*P. oxalidosum* to *P. sphagnosum*). The two series in the end lead to the same thing—the extermination of the spruce forests and their replacement by moss bogs. In both cases the process, according to the concomitant external conditions, may proceed sometimes more rapidly, sometimes more slowly, lingering or stopping at certain stages.

Some of the other communities of the first four groups clearly enter into certain of the successions described. *Piceetum alnoso-caricosum*, for example, being allied to *P. fontinale* also changes into *P. sphagnoso-herbosum* and later into moss bog. But just as in the second series described the communities generally succeed each other less rapidly in the progress to bog, so *P. alnoso-caricosum* too may for a considerable time maintain itself on an area.

Let us turn to the consideration of the interrelations in the group *P. fruticosa*. Since the two communities which have been distinguished as belonging to it are closely linked, the limit between them is an artificial one, and since the group is characterised by the intrusion of broad-leaved species, the elucidation of the interrelations between the two communities as well as those between them and other *Piceeta* is equivalent to the elucidation of the interrelations between the spruce and these broad-leaved species, among which the oak occupies the fundamental position. Therefore it is a question of the interrelations between the spruce and the oak. On this question there are extant a series of works by Russian investigators, botanists as well as specialists in forestry, among which those by S. T. Korzhinski, G. F. Morosov and A. I. Gordyagin are the most important.

Comparing all that has been written on this subject, it must be recognised that the oak and its concomitants are supplanted by the spruce, and that the group of *Piceeta fruticosa* is but a stage in this process. The process is however a slow one, in which the victory of the spruce over the oak is brought about not only by the shade resistance of *Picea* but by other peculiarities, among which is its influence on the soil. Thus *Piceetum querceto-tiliosum* may remain without sharp change during several generations and even sometimes owing to fortuitous causes, e.g. an attack of bark-beetles on the spruce, may undergo temporary alterations in the opposite direction, i.e. towards the predominance of the oak and its concomitants. Nevertheless the final result will be the supplanting of the broad-leaved species by the spruce, together with the replacement of grey forest-soils and soils resembling the black earth, characteristic of the oak, by podsol-soils.

This process of the supplanting of deciduous summer forest by spruce forest connected with the gradual degradation of the soils is generally marked

by a dropping out of the oak and its concomitants, the first to disappear being the ash, followed by the oak and the maple, the last being the lime. *Tilia cordata*, being the most shade resistant and the least exacting as to soil (satisfied even with the podsol-soil) holds on the longest, assuming in the end the form of a shrub stratum in the community *Piceetum tiliosum*. This must be considered as the last stage in the supplanting of broad-leaved by spruce forests; and the lime, as G. F. Morosov put it, "is the witness, as it were, of those times when in a certain region there lived an oak forest." Logically we must admit that a further step in this process, in connection with a further impoverishment of the soil, will be the dropping out of the lime also, together with the rest of the shrub stratum of the oak forest, the impoverishment of the herb flora and the development of a continuous moss stratum, i.e. the formation of *P. oxalidosum*, which, as it were, rounds off the whole succession.

From the preceding characterisation of spruce forest it is evident that the fundamental type, in which the most important features of spruce forest are expressed most completely, is the group of *Piceeta hylocomiosa*. The other groups include either communities formed under conditions of excessive moisture, not characteristic of the usual life conditions of the spruce, or under the influence of conditions nearer to those of broad-leaved forest, and consequently also not characteristic of the spruce. We see, as it were, three fundamental ecological series of communities¹, originating from the group *P. hylocomiosa*. One of them is connected with the beginning of excessive water supply together with stagnation of the water, i.e. a worse supply of oxygen to the roots and deterioration in the supply of mineral food—this is the series *P. hylocomiosa*—*P. polytrichosa*—*P. sphagnosa*. The second series, too, is connected with excessive moisture, but the water is in motion and the roots, consequently, are sufficiently supplied with oxygen, while the mineral food supply is not always improved—this is the series *P. hylocomiosa*—*P. herbosa*. The third series is connected with an improvement of the mineral food supply without a change in the water régime of the habitat or (and this is the commoner case) with a certain increase of dryness and consequently without deterioration and even with improvement of the supply of the roots with oxygen—this is the series *P. hylocomiosa*—*P. fruticosa*.

In each of these groups there is one principal community in which the characters of the group are represented most typically. Next to this come the communities connected with conditions usually already changing in the direction of an approach to the conditions of another group. This leads to an approach of the structure of the community of the given group to the structure of another group. Here within the limits of each group series of two categories are suggested:

¹ The idea of distinguishing ecological series of communities for the purpose of studying the vegetation was first advanced (in Russia) by B. A. Keller, and later by V. V. Alekhin, B. N. Gorodkov, and some other Russian authors.

(1) *ecological-edaphic series* connected with a change of the nature of the soil within the limits of a definite region.

(2) *ecological-geographic*, or more exactly *ecological-climatic series*.

Each series will represent vicarious associations.

It has been already mentioned that at the present time it is difficult to give even an approximately complete list of these series and of the principal communities composing them, still less of the subordinate communities, owing to the fact that the spruce forests have been little studied from the phytosociological point of view. We have been able to give only instances illustrating general propositions. But these fundamental ideas must serve as a guide in the further investigation of the spruce forests. Then the establishment of new spruce associations, even if their number be considerable, or the subdivision of the old ones, notwithstanding inevitable subjectiveness in their extent and distinction, will not produce confusion, and the different grades of community distinguished will form a definite system.

On further consideration of the examples of communities given for each group, it may be seen that in the fundamental group *Piceeta hylocomiosa*, the principal community is *P. oxalidosum*. This realises most completely the type of spruce forest in general. Here the rôle of the spruce as the "builder" of the community finds its strongest expression. Within the limits of this group we see the series moving through *P. myrtillosum* in the direction of somewhat greater moisture and decrease of oxygen supply, i.e. in the direction of *P. polytrichosa*. Another series leads, on the contrary, in the direction of an amelioration of the mineral régime of the soil; here belong *P. polytrichosum* and *P. atragenoso-oxalidosum*, though neither of these communities have been sufficiently investigated. This series leads to the group *P. fruticosa*. Finally *P. empetroso-vaccinosum* concludes the ecological-climatic series, where it is vicarious climatically with *P. oxalidosum* and *P. myrtillosum*.

In the second group the principal community is *P. polytrichosum*, with which *P. empetroso-polytrichosum* forms an ecological-climatic series. Further investigation will show whether within the limits of this group there may be distinguished ecological-edaphic vicarious communities or whether *P. polytrichosum* is so persistent and sharply delineated that there are no others.

In the third group the principal community is *P. sphagnosum*, with *P. caricoso-sphagnosum* on the side leading to *P. herbosa*, thus forming an ecological-edaphic series determined by ameliorated oxygen supply of the roots resulting from a less complete stagnation of the water.

In the fourth group, where the principal community is doubtless *P. fontinale*, *P. sphagnoso-herbosum* on the contrary finds itself in the series of deteriorating oxygen supply of the roots, i.e. diminished flow of the water. Thus we have within the limits of the two last groups the following series: *P. sphagnosum*—*P. caricoso-sphagnosum*—*P. sphagnoso-herbosum*—*P. fontinale*, connected with an increase of the water flow, where the extreme members

are phytosociologically very sharply distinguished, while the two intermediate ones form connecting links between them. To separate these two groups by tracing the limit between the two inner members would, of course, be somewhat arbitrary.

Finally the principal community of the fifth group is *P. tiliosum*, and *P. quercoso-tiliosum* has its place in the series determined by an amelioration of the mineral régime and further leading to broad-leaved forest. These ecological series of *Piceeta*, leaving out of consideration the ecological climatic vicarious associations and limiting ourselves to the ecological-edaphic series, may be represented as in the diagram on p. 5¹.

On closer examination of these series we see that they correspond not only with the ecological but also the genetical connections of the communities. The process of succession takes its course along these very series. So the series, let us call it the series A, connected with alteration of the nutritive mineral content of the soil and the absence of excessive moisture is in its essence a succession from oak forest communities to typical *Piceeta*, being the result of the impoverishment of the soil due to the influence of the forest communities themselves and characterised by the clearing from the *Piceeta* of the alien elements of broad-leaved forest. This series leads to the formation of the most characteristic association of *Piceeta*—*P. oxalidosum*.

The series B, leading in the direction of increased moisture and its stagnation, is the succession of *Piceeta* to bog. If the impulse to its appearance is usually given by external factors, its whole further course is connected with a change of environment produced by the plant communities themselves. Thus their own action on the environment is the chief cause of the succession of communities in this series.

The median series C, on the contrary, has its origin in communities dependent on excessive soil moisture and running water; it is a succession whose fundamental cause is the change in the external factors of existence, the influence of the plant communities on the environment taking no considerable part in the process. In this series, developing parallel to the development of the valley of the rivulet or brook and the deepening of its bed, and hence to the draining of the bottom of the valley, we have a succession to the community *P. fontinale* from communities of the group *P. hylocomiosa* and ultimately from *P. oxalidosum*.

¹ It seems possible to establish one more series of communities, again beginning with *P. oxalidosum* and dependent on increasing depletion of the soil in nutritive material, but without any increase in its moisture. To this series may be referred the spruce forest with a dominant herb stratum composed of *Vaccinium vitis-idaea* (*Piceetum vacciniosum*), which the Finnish authors usually identify as "Vaccinium-type" (VT). According to the statement of A. P. Shennikov, the well-known investigator of Northern Russia, this community proves to be fairly common in some localities of the province of Archangel. Nevertheless there exist as yet no descriptions of it in the Russian literature; I have therefore had to withhold any detailed characteristics. This community undoubtedly belongs in the group of *P. hylocomiosa*, differing from *P. oxalidosum* in greater dryness of the soil. A further study of this series (E) is very desirable.

If the succession from *P. fontinale* is determined, not by a gradual drying of the soil, but by impeded flow of water and gradual accumulation of peat deposits, we shall have the series D, i.e. the succession from *P. fontinale* to *P. sphagnosa* and then to pure bog.

The geographically vicarious communities which form ecological-climatic series are here left without discussion because they are almost uninvestigated. But they also must represent genetical series in a certain sense, i.e. communities succeeding one another when the climate changes in the course of time. If we wanted to present in one diagram these ecological-climatic series as well as the ecological-edaphic ones, the most convenient way would be to trace them upwards and downwards from the latter communities represented on a plane, i.e. to plot our diagram in three dimensions.

If we take into consideration that the series of *Piceeta* under discussion represent also successive changes of the structure (morphology) of the communities and the interaction of the members of which they are composed, we shall be fully justified in calling them also phytosociological series.

The farther in each series a community is from the *P. oxalidosum* the weaker is the rôle of the spruce as the "builder" of the association, and the more prominent on the contrary are the importance of the other elements of the community, which in their nature are alien to the type community *P. oxalidosum*. In the series A such a rôle is played by the broad-leaved species, in the series B by *Sphagnum*, and in the series C by the herb stratum.

With an improvement in the quality of the soil, according to which the ecological series was established, we shall obtain communities where the spruce is already absent, being supplanted by another "builder" (*édificateur* of Braun-Blanquet). Thus in the series A such a community will be the broad-leaved forest with the oak and its concomitant species, in the series B *Sphagnum* bog with gnarled and stunted pine, an association in which the "builder" is *Sphagnum*, and in the series C the grassy bog.

Although, chiefly from the morphological point of view, we have established five groups of *Piceeta*, it would perhaps be more correct from the phytosociological and genetic standpoints to establish only four, considering *P. polytrichosa* as transitory associations between *P. hylocomiosa* and *P. sphagnosa* and including them in the fundamental group of *P. hylocomiosa*, as the nearest links to *P. myrtillosum*.

It was pointed out above that the *P. herbosa* may, under certain conditions, be genetically succeeded by communities of the group *P. sphagnosa*. It is, however, theoretically quite imaginable that *P. herbosa* would pass over into *P. fruticosa*, viz. when in the *P. herbosa* there is an abundance of running water combined to very rich soil, and when after the natural draining of the land owing to the development of the river valley the soil remained as rich as it was before. But such successions are not as yet described, and connecting links between these groups have not been observed.

Thus we see that the establishment of ecological series of spruce communities gives us a clear idea of the phytosociological and genetical interrelations between these communities.

Further, the same series allow us to foresee, within certain limits, the character of new communities, not yet known or described, but which may be detected in the future. Thus communities connecting *P. oxalidosum* and *P. fontinale* are not yet known, but no doubt they must exist since there are thinkable transitional natural conditions between those peculiar to these communities in their typical forms. Since we are already acquainted with the extreme members of this series we may in some degree imagine the composition and structure of intermediate links yet to be discovered. The same applies also to the other series, where we are far from knowing all the members.

Hence, it seems to me, it can be seen that the method of ecological series may have a much more extensive significance than that of elucidating the connection of the vegetation series with environment. In its further development it promises to be of assistance in the construction of such a system of communities, as will offer not only a harmonious picture of the phytosociological and genetical interrelations between them, but will allow us to foretell the existence and character of communities not yet described.

THE VEGETATION OF ALBERTA

II. THE SWAMP, MOOR AND BOG FOREST VEGETATION OF CENTRAL ALBERTA

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(With Plates I-XI, a Folding Map and eight Figures in the Text.)

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INTRODUCTION.

THIS investigation is a continuation of a paper published in 1926 in this JOURNAL (1) and is the second of a series which we hope to publish on the vegetation of Alberta from an ecological standpoint. It is designed to carry out this work on a monographic basis, taking the various vegetation formations

in different parts of the Province and describing the associations and their succession within the formations.

Attention has first been centred on the associations in the moor series as these are a prominent feature both in the northern part of the Parkland belt and the coniferous forest to the north and west of Edmonton.

The regions to be described in this and subsequent papers are of large area and the vegetation associations unknown, and the work is therefore in the nature of a primary survey. It is felt under these conditions that a broader consideration and correlation of the main grouping of vegetation and succession can be better obtained by a more generalised treatment of associations rather than by subdividing. Particular attention has been paid to the general trend of hydrarch successions. Many factors have interfered with this normal succession; fire, changes in drainage, biotic factors have played and are still playing their part, frequently destroying the sub-climaxes and producing a variety of secondary successions.

In the Parkland some attention has been given to effects of burning, drainage, pasturing and mowing upon the development of vegetation. Detailed investigation of these factors may be expected to yield results of considerable ecological interest and of economic importance in agriculture.

In the course of the work hydrogen-ion determinations and analyses of the water have been made.

Observations on the stratification of the peat layers have been carried out for some bogs, and, wherever possible, sections or borings made to the base of the peat and an analysis made of the underlying clays. The fossil remains in the clays have been examined, and it is expected that such remains—which are not infrequent—will, as the work progresses, throw light on the early history of vegetation in post-glacial times.

During the field work certain extensive deposits consisting of over 80 per cent. calcium carbonate have been found associated with the peat, and these are likely to prove extremely valuable in the treatment of certain types of soils common in the west-central part of the province.

So far, the utilisation of extensive peat areas for economic purposes has not been necessary, but this will undoubtedly take place at some future time; and therefore a knowledge of the history of the deposits, the succession of vegetation, and the chemical and physical characters of the water and the underlying deposits, will certainly prove valuable from an economic point of view.

The nearest bog successions which have been investigated on the above plan are in Minnesota, and the examination of areas situated 1100 miles (1770 km.) north-west in a different topography and climate and characterised by different types of climax vegetation will yield results of ecological interest.

MAP OF
THE PROVINCE OF
ALBERTA
CANADA

showing the main

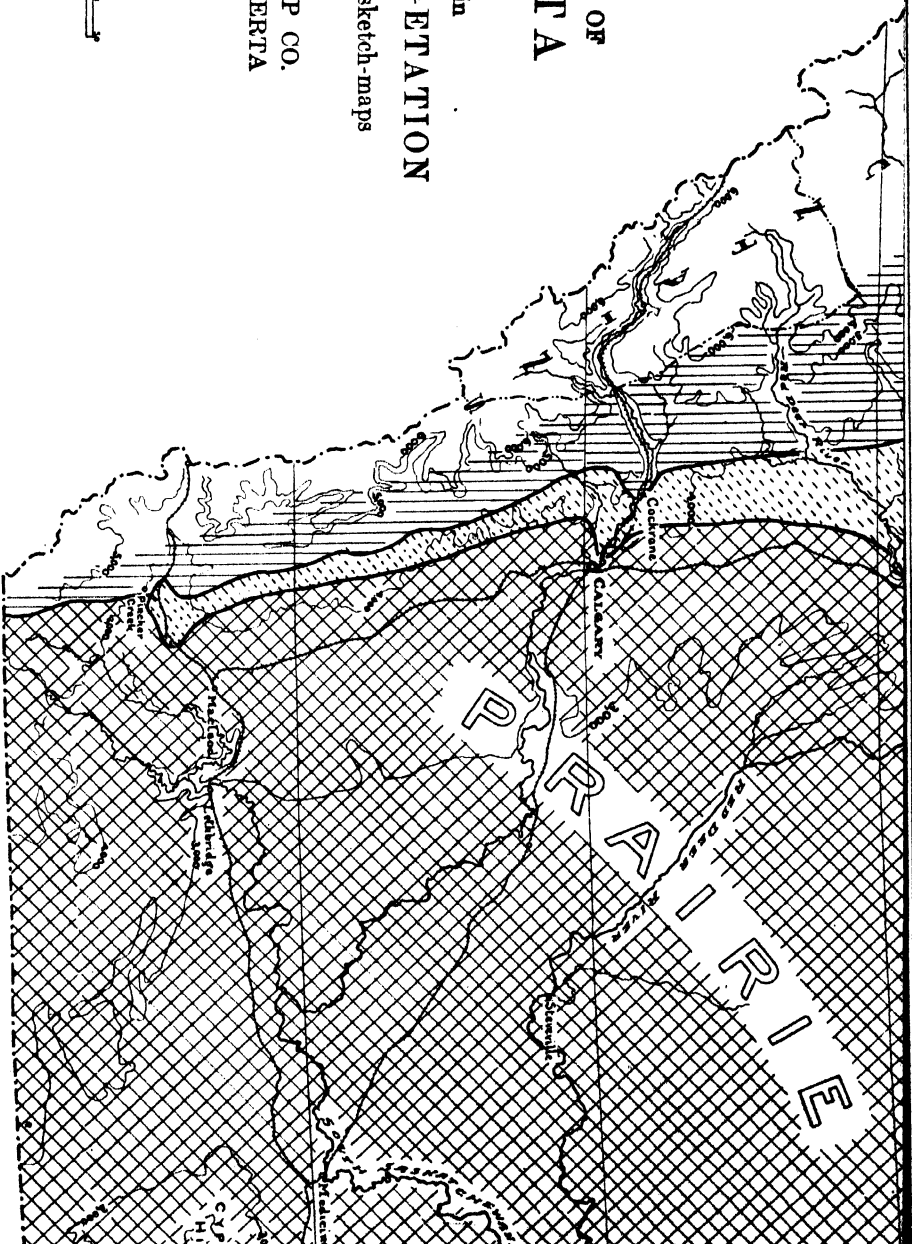
REGIONS OF VEGETATION

drawn from the authors' sketch-maps

by

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EDMONTON, ALBERTA

Scale of Miles
0 1 2 3 4 5 6 7 8 9 10



THE CLIMATIC FORMATIONS OF ALBERTA.

A brief description of the salient features of the climatic formations of the province may be given here, as it will serve to illustrate some of the features to be described later. Stretching from the 60th parallel to the 49th parallel (the International boundary), the province comprises within this area a considerable diversity of vegetation from the northern coniferous forest to semi-arid prairie in the south. Westward, it extends to the divide of the Rocky Mountains which form the boundary for 450 miles (727 km.), north of which the western boundary runs on the 120th meridian for 408 miles (657 km.). The eastern boundary is marked by the 110th meridian. There are four broad climatic formations in this area whose boundaries are shown in Map 1. This map has been compiled chiefly from the vegetation map given in the Atlas of Canada, 1915 (2), and from various other sources and partly from our field observations for 200 miles (320 km.) round Edmonton. The boundaries are at present approximate and only serve to indicate the main trend of the climatic formations.

THE NORTHERN FOREST.

This is continuous with the coniferous forest whose distribution stretches from Labrador and Newfoundland to the Rocky Mountains and northward to Alaska and forming (with the elimination of certain more southern species) the forest line in the arctic regions. In the area covered by the map the forest consists mainly of the following trees:

Picea albertiana Stew. Br.

P. mariana (Mill) B.S.P.

Pinus banksiana Lamb.

Larix laricina (Du Roi) Koch

Abies balsamea (L.) Mill

Populus tremuloides Michx.

Populus balsamifera L.

Betula papyrifera Michx.

But the grouping of these trees and their relative abundance are to a large extent unknown. In the neighbourhood of the Parkland the dominant tree is *Populus*, except on the peat areas, where *Picea mariana*, *P. albertiana* and *Larix laricina* are typical. In an area considered in a later section of this paper *Pinus banksiana* appears to be the dominant type and covers large areas on sandy soil and stabilised sand-hills in the country south of the Athabasca River. No evidence of this tree forming the climax type on the muskegs has yet been met with, though little invasion of *Pinus banksiana* forest by *Populus* appears to be taking place.

THE CORDILLERAN FOREST.

This phytogeographical region is marked by the gradual disappearance of most of the trees of the Atlantic type and their replacement by trees belonging to the Pacific floral province. As might be expected, the change is gradual and there is much overlapping, but the boundary is rendered more obvious by the dominance of *Pinus Banksiana* in the northern coniferous

forest and of *Pinus contorta* in the Cordilleran formation. The two species only overlap to the east of the Lesser Slave Lake and as far south as Athabasca. The chief trees are:

Pinus contorta Dougl.

P. albicaulis Engelm. (at higher levels towards the mountains)

Picea albertiana (Mill) B.S.P.

P. engelmanni (Parry) Engel.

Pseudotsuga douglasii Carr.

Abies lasiocarpa (Hook) Nutt. (at higher levels towards the mountains)

The most characteristic tree in the Cordilleran forest, to the west of Edmonton, is *Pinus contorta*. In travelling west from Edmonton to the border of the Parkland it is interesting to notice the earliest appearance of this tree, at first isolated specimens and then small clumps developing into groves until, a few miles west of Pembina River, it becomes dominant. The actual distance from the first isolated trees to the point where this species becomes dominant on non-peat-covered lands is 44 miles (71 km.), this affording an interesting illustration of the actual breadth of transition which may occur in passing from one great phytogeographical region to another.

Towards forest line in the mountains other climax types of vegetation make their appearance, but a discussion of these is outside the scope of this paper.

The country lying within the region of the Cordilleran Forest, discussed in this paper, bears every evidence of having been burnt, and, although *Pinus contorta* is now the dominant tree, the evidence at present available does not point to its being the climax stage. In the mountain valleys *Pinus contorta* is always the tree characteristic of burnt over areas and this appears to be so in regions as far south as Colorado (3). In the valleys of the Rocky Mountains miles of slopes lying between 4000 ft. and 6500 ft. (1220 m. and 1980 m.) are covered with a pure forest of this species, and on mountain sides in which the original spruce (*Picea albertiana*) has been burnt off *Pinus contorta* invariably makes its appearance. Some evidence to be discussed later in this paper suggests that *Picea albertiana*, *P. mariana* forest, is the true climax in this region of the Cordilleran forest with *Picea engelmanni* as the mountains are approached. More detailed evidence on this point may be gained when areas nearer the mountains are investigated. Northward of McLeod River the vegetation has evidently been decimated by fire in past ages and the vegetation presents a confused appearance, groves of *Picea engelmanni* which have escaped burning alternating with patches of *Pinus contorta*, *Picea albertiana* and open Parkland and bog. This region so fundamentally different to the Parkland, both in topography and in soil, has been subjected to invasion and re-invasion in which vegetation of the alpine and sub-alpine regions of the mountains, the Cordilleran forest and the Northern Coniferous forest regions, have participated, and now presents a veritable "no man's land" of vegetation.

THE PARKLAND.

A brief note on the general vegetation of the Parkland in the neighbourhood of Edmonton was given in a former paper (1). It may be doubted whether this belt which separates the coniferous forest from the prairie region can be truly considered as a climatic formation. Although the soil and topography of the country simulates prairie, two characteristic trees of the Northern Coniferous area are present, *Picea albertiana* and *P. mariana*; the former is usually found along ravines and the latter on muskegs. Much of the general vegetation is that characteristic of the northern forest and it appears reasonable to regard the Parkland as a transition belt, where slight differences of soil, climate and topography, have allowed grassland to become invaded by the northern vegetation, these special conditions giving the preference to *Populus tremuloides* and other members of the Salicaceae and where conditions offer a suitable habitat, by two of the characteristic trees of the northern forest. More definite evidence on these points will probably be forthcoming when ecological investigations on the Parkland are available.

GENERAL TOPOGRAPHICAL FEATURES OF ALBERTA

The Province may be divided into two main regions, (1) a western portion culminating in the central ridge of the Rocky Mountains with elevations varying from 8000 ft. to 13,000 ft. (2440 m. to 3965 m.) with a region of foothills about 30 miles (48 km.) in width with elevations from 4000-5000 ft. (1220-1525 m.); (2) an undulating plateau with elevations of 3000 ft. (915 m.) in the south and west which gradually falls towards the east and north where a general elevation of 700 ft. (215 m.) is reached. Excepting the Cordilleran region, the only sharp relief is met with in the several great river valleys which run east and north where gorges and lateral valleys with steep sides are a usual feature. Such valleys usually show a marked difference in vegetation to the plateau land.

Throughout the area, except in the mountain region and on the sides of the larger river valleys, there is very little relief sufficiently sharp to influence the vegetation. Owing to the latitude and the exceeding dryness of the air, the actual inclination of the ground has a great effect on the amount of heat and light received from the sun. On the north and south-facing sides of the large river valleys, where the inclination may be 30°-45°, great differences in vegetation may be remarked, and we might expect a far greater diversity of the vegetation on the plateau if slopes of greater inclination were common.

Lakes are extremely numerous in certain regions of the plateau. These are, for the most part, mere shallow basins in the superficial deposits and may be partially dried up during a long hot summer season. The larger ones, such as Cooking Lake, Wabamun Lake, and a host of others, are permanent bodies of water, and depths of 40-70 ft. (12.2-21.3 m.) are not uncommon in those

which have been sounded. In the majority of cases these depths appear to be due to hollows in the superficial deposits and not to excavation by glacial action.

In the Northern forest lakes of all sizes dot the surface of the country, varying from a few hundred yards in diameter to deep large lakes like Lake La Biche, 18 miles (29 km.) long and 16 miles (26 km.) wide, Lake Athabasca, 160 miles (260 km.) long, Lesser Slave Lake, 50 miles (80 km.) long. In regard to some of these larger lakes, it is known that they lie in rock-basins. Other narrow winding lakes occupy the whole width of a narrow valley, such as Coal Lake, 12 miles (19 km.) long and $\frac{3}{4}$ mile (1.2 km.) in width. A lake of this type is really a local extension of a stream draining a valley and dammed up for a certain distance by superficial deposits.

In the prairie area lakes are numerous, although generally shallower and smaller in size than in the above mentioned districts.

RAINFALL.

Yearly rainfalls for some stations in the Parkland areas described in this paper were given in a former paper. These may be quoted again together with other stations situated in the forest areas described now:

Annual Precipitation (inches).

| | | 1921 | 1922 | 1923 | 1924 | 1925 | Average |
|-----------|-----|-------|-------|-------|-------|-------|---------|
| Athabasca | ... | 14.69 | 13.44 | 14.95 | 18.34 | 16.55 | 15.59 |
| Meanook | ... | 15.14 | 11.67 | 14.45 | 19.13 | 16.61 | 15.40 |
| Edmonton | ... | 15.10 | 13.73 | 17.42 | 18.41 | 17.44 | 16.42 |
| Red Deer | ... | — | 12.21 | 22.92 | 20.07 | 21.87 | — |
| Edson | ... | 16.61 | 12.12 | 14.99 | 20.38 | 22.29 | 17.27 |
| Entrance | ... | 14.34 | 10.75 | 14.51 | 13.52 | 21.12 | 14.84 |

It is not safe to generalise from so short a range of observations as given above. The records are available much farther back at Edmonton, but since most of the other stations give incomplete returns earlier than 1920 a longer comparison cannot be made. The figures do show that the ranges between different years at the same station are much greater than the ranges between different stations during the same year.

The differences recorded at these stations, which cover 200 miles (320 km.) north to south and 130 miles (210 km.) east to west, would not seem sufficient greatly to affect vegetation. Careful analysis would probably show considerable differences between the forms, and some differences between the times, of the precipitation at the stations, and these might be sufficient to leave an impress on the vegetation.

The humidity of the air and the rate of evaporation probably varies relatively much more than the rainfall but, in the absence of such records and readings with atmometers, there are no actual figures to support this conjecture. The high rate of evaporation may be gauged by the features shown by the snow during the spring thaw where under-cut banks and little mush-

room-like pinnacles often occur facing the prevalent wind. This is not due to drifting but to evaporation. An interesting illustration of the power of the sun and the coolness of the air is shown each year on tennis-courts on the University grounds. These are enclosed by a wire-netting fence which has a horizontal bracing timber $1\frac{1}{2}$ inches (3.8 cm.) deep by $3\frac{1}{2}$ inches (8.9 cm.) wide, and 5 feet (1.5 m.) from the ground. On the side facing south the shadow of the horizontal bar results in a bank of snow being left after the rest of the tennis court is free from snow. A photograph taken March 26th, 1927, is shown in Pl. I, Phot. 1, where the vertical side of the ridge facing the south is $6\frac{1}{2}$ inches (16.5 cm.) high.

THE CORDILLERAN AREA.

Before any detailed description of definite areas is given, the xerarch and hydrarch series may be briefly discussed, in order to point out the general features of the climax stage.

The district examined during 1926 is a strip of country between Pembina and McLeod Rivers covering a distance of about 75 miles (120 km.). This district is heavily covered with glacial drift which forms series of gently rolling sandhills and sandy depressions clothed for the most part with open woods of *Pinus contorta*. At the eastern end of this piece of country lies Chip Lake and from here westward to McLeod River wind stretches of low lying ground about 1 mile (1.6 km.) in width which appear to be old extensions of Chip Lake. The depressions are now occupied by muskeg and heavily forested with black spruce. A brief résumé of the associations of the xerarch and hydrarch series from a general point of view will be useful in arranging the numerous associations of this area in a successional order. With this object we shall consider first, a secondary xerarch succession of the upland, and second, primary hydrarch successions of the lowland.

The first type of succession can be best seen on the burnt over sand-hills. The first vegetation to appear here after burning is usually a *Populus tremuloides* association which is rapidly succeeded by *Pinus contorta*. The latter is the most common tree of the district, because fires are here prevalent enough to keep the subsequent stage in check.

The pine is usually found in open formation rather than in the thick stand in which it grows farther westward. This habit may be correlated with the poor sandy soil.

The presence of the trees only slightly modifies the amount of sunlight beneath, so that there is a thick carpet of xerophytic, sun-loving, herbaceous plants and in the more open spaces, even of shrubs. The dominant plant of the undergrowth is *Arctostaphylos uva-ursi* (L.) Spreng.; *Vaccinium vitis-idaea* L. and *V. canadense* Richards are abundant and are associated with *Hieracium canadense* Michx., *Viburnum pauciflorum* (Robbins) Britt., *Comandra richardsoniana* Fernald. These cover the floor of the forest, while in the more

open parts are found *Shepherdia canadensis* Nutt., *Ledum latifolium* Ait., *Amelanchier* sp., *Rosa* sp., and *Populus tremuloides* Michx.

This association may in time become succeeded by a forest of *Picea mariana* (Mill) B.S.P., the trees growing thickly and casting a dense shade, so that the undergrowth is limited to mosses. Although this mature forest is rare in the district, many cases can be seen of the invasion of the young black spruce into the pine association. The spruces first take possession of the base of the hill where conditions are most mesophytic, and from here the seedlings gradually ascend to the summit. This is illustrated in Pl. II, Phot. 4, where the black spruce is seen on the lower slopes of the sandhills above McLeod bog (p. 32).

In this district we have a complex of two extreme and sharply contrasted habitats, bog, and sandhill. On each of these the vegetation sequence has been arrested, on the lowlands because of poor drainage, and on the uplands because of frequent fires. We may however consider the climax association to consist of *Picea mariana* forest with an undergrowth of *Hypnum*. The only exception to this is along the river courses, where any well shaded ravine is occupied by *Picea albertiana* Stew. Br. which may be looked upon as a post-climax, only reached in super-mesophytic conditions.

The tree is not present on the sandy soil of the upland and cannot compete with the black spruce in range of adaptability or acid tolerance, so offers little competition with the latter on bog or sandhill.

The thickly growing trees of the white spruce forest shelter the following shade tolerant mesophytes:

| | |
|--|---|
| <i>Lycopodium annotinum</i> L. | <i>Polygonatum giganteum</i> Dietr. |
| <i>Streptopus distortus</i> Michx. | <i>Actaea alba</i> (L.) Mill |
| <i>Microstylis ophioglossoides</i> Nutt. | <i>Mertensia paniculata</i> (Ait.) Don. |
| <i>Cypripedium spectabile</i> Salisb. | <i>Cornus canadensis</i> L. |
| <i>Viburnum pauciflorum</i> (Robbins) Britt. | <i>Linnaea borealis</i> L. |
| <i>Delphinium brownii</i> Rydb. | <i>Pirola secunda</i> L. |
| <i>Symphoricarpos pauciflorus</i> (Robbins) Britt. | <i>Mitella nuda</i> L. |
| <i>Aquilegia canadensis</i> L. | |

Such white spruce associations are common in small groves in the poplar woods along the slopes of the McLeod River Valley. That they represent the climax of a bog series is shown by an examination of these spruce thickets in their young and mature stages.

It was found that before the appearance of spruce, these depressions are occupied by willows and aquatic grasses and sedges. As the pools of water begin to dry, *Sphagnum* and ericaceous plants such as *Ledum* invade these low moors, forming small *Ledum* moors. These in turn give way to white spruce woods, in which the *Sphagnum* undergrowth is gradually replaced by *Hypnum* and *Hylocomium* and the mesophytic plants of the white spruce forest.

The most valuable evidence for the interpretation of the normal hydrarch successions is, however, obtained from the examination of lake margins. The table (p. 27) shows three types from this country:



Phot. 1. Snow ridge facing south caused by shadow falling from cross-bar of fence on left. March 26th, 1927 (p. 25).



Phot. 2. *Picea mariana* invading *Pinus contorta* on sandhills above McLeod bog (p. 26).

Table showing the associations of lake margins.

| Lake No. 1 Illustrating the most widely distributed type | Lake No. 2 Common in the Athabasca area | Lake No. 3 McLeod bog, illustrating the maximum number of successions |
|--|---|--|
| 1. Lake | 1. Lake | 1. Lake |
| 2. Low-moor (<i>Carex-Hypnum</i> association) | 2. — | 2. Low-moor |
| 3. — | 3. Birch bog (telescoping of <i>Betula-Hypnum</i> and 4. <i>Larix-Hypnum</i> associa- tions) | 3. <i>Betula-Hypnum</i> association |
| 4. — | | 4. <i>Larix-Hypnum</i> association |
| 5. <i>Ledum</i> moor (<i>Ledum</i> , <i>Sphagnum</i> , young <i>Picea</i> <i>mariana</i> association) | 5. <i>Ledum</i> moor | 5. <i>Ledum</i> moor |
| 6. — | 6. — | 6. Young bog forest (mature <i>Picea mariana-Ledum- Sphagnum</i> association) |
| 7. — | 7. — | 7. Mature bog forest (<i>Picea mariana-Hylocomium</i> as- sociation) |
| 8. Climax forest | 8. Climax forest | 8. Climax forest |

Since the last type includes the full series of successions, such a type from the Carrot Creek area will be described.

A small irregular lake is surrounded by concentric bands of different types of vegetation and these may be described, beginning with the aquatic vegetation and proceeding centrifugally:

1. The aquatic stage. Here *Ranunculus aquatilis* L. is the dominant plant.

2. The low-moor stage. This occurs in a band about ten yards wide. It stands several inches in water. *Carex aquatilis* Wahl. and *C. diandra* Schrank. are dominant, associated with considerable quantities of *Hypnum*.

3. (a) The birch moor stage. This narrow band of moor is dominated by *Betula glandulosa* Michx. *Sphagnum* is invading the band from the outer edge.

(b) The larch moor stage. This band is a swamp, extending back about fifty yards. The larch is accompanied by *Betula glandulosa* and an undergrowth of *Sphagnum acutifolium* var. *versicolor* Warnst. As these two stages (3 (a) and 3 (b)) are very seldom separated, the two are collectively considered as birch moor.

4. The muskeg series:

(a) The *Ledum* moor stage. The mat of *Sphagnum* of the young muskeg fronting the lake supports a collection of ericaceous plants and a quantity of seedling black spruce.

(b) The young bog forest stage. In this stage the undergrowth of *Sphagnum* and *Ledum*, etc. is unchanged, but the trees have attained their full size.

(c) The mature bog forest stage. Here the *Sphagnum* of the younger forest is replaced by *Hypnum*. The peat has become decomposed, and broad-leaved plants have replaced the ericaceous undergrowth.

5. *The climax forest.* With the drying up of the pools of water in the bog forest and the elimination of the more hydrophytic plants of the undergrowth, the climax association of the district is attained.

These preliminary observations may be of use in giving a proper perspective to the various areas now to be described. The principal hydrarch stages to be met with are as follows:

1. Aquatic stage.
2. Low moor.
3. Birch moor.
4. Muskeg:
 - (a) *Ledum* moor.
 - (b) Young bog forest.
 - (c) Mature bog forest.
5. Climax forest.

The first areas to be described are low-moors originating from sloughs in the forest, followed by a description of the invasion of low-moor by *Sphagnum* in the absence of the intermediate birch moor. The third type of associations represent birch moors, while the fourth illustrate the characteristic bog forests.

The Low Moors.

The drying of sloughs in the forest frequently results in the formation of small low-moors. Between the sand hills many of these distinct vegetation units are met with in small depressions about 300 ft. (91.5 m.) in diameter. They do not differ materially from low-moors in the Parkland described on p. 56. They are largely *Cariceta* dominated by *Carex diandra* Schrank. with *C. aquatilis* Wahl. subdominant and *Hypnum* forming a mat below. Some of these low-moors, like those described elsewhere, are bounded by muskeg vegetation invading the low-moor centripetally. Others in a more advanced stage of development show no hint of this but are surrounded on the outside by a Graminetum dominated by *Calamagrostis canadensis* with *Glyceria* locally subdominant.

While little evidence of active *Sphagnum* growth at the present time is to be seen on the low-moors in the areas described from east and south of Edmonton, the country north and west affords numerous examples of active *Sphagnum* bogs. Most of them described in this paper are marginal to low-moors and their development is mainly centripetal. It will be of interest to describe one in which the *Sphagnum* bog is central, surrounded by low-moor and whose growth is therefore centrifugal. The features shown by this bog are unique for the areas we have investigated, and, although this bog is just within the western limit of the Parkland, it may be more fittingly described here.

The general topographical features of this area are shown in Fig. 1. The

bog lies in a well marked basin defined by a long curving moraine to the east and lower ground on the west and south, while the constricted northern end

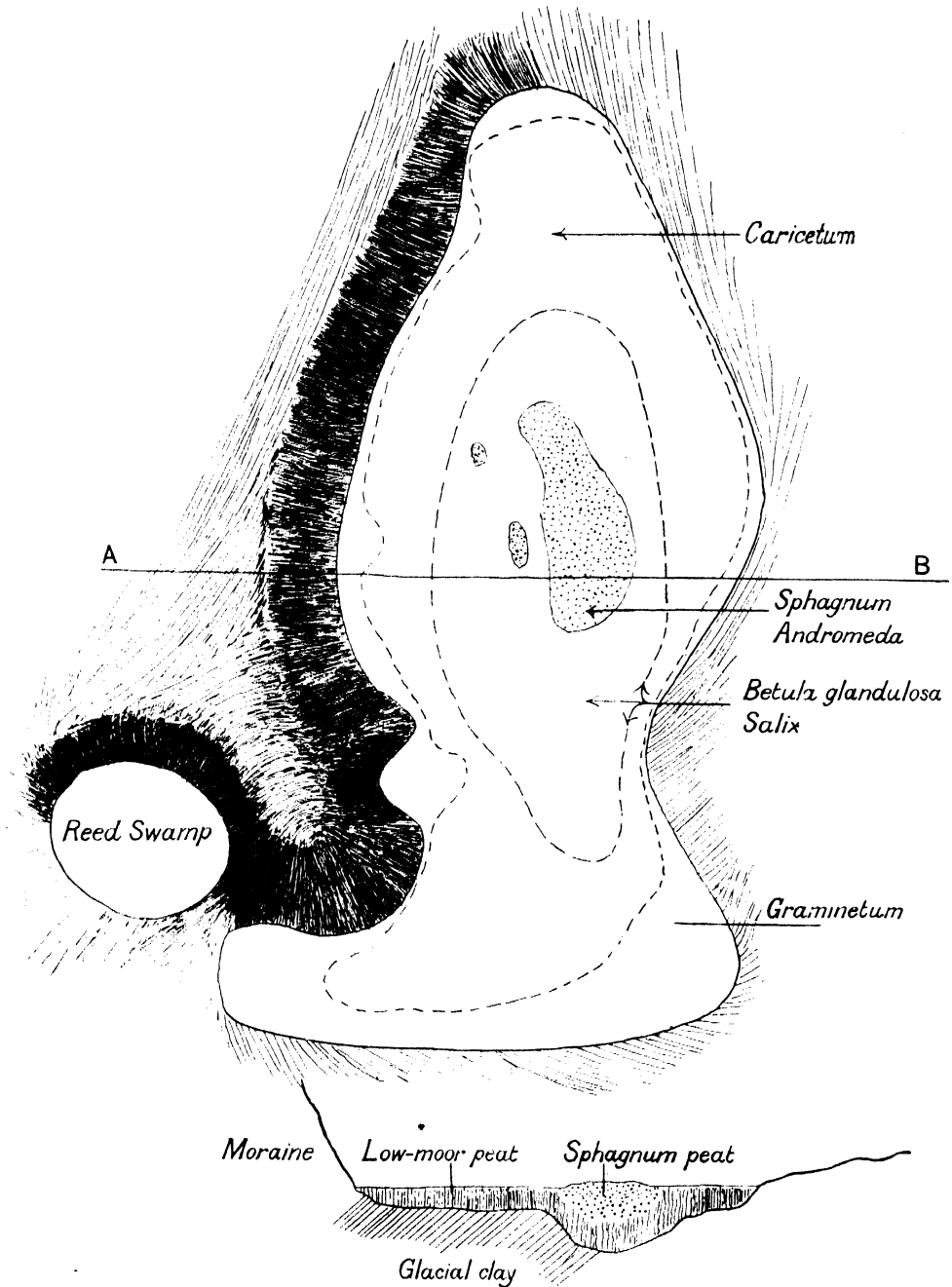


FIG. 1. Topography and vegetation of low-moor showing centrifugal spread of *Sphagnum*.

is enclosed by ground rising only 1 or 2 ft. (30 or 60 m.) above the surface of the bog.

This main basin is in close proximity although not in connection with a small deep depression or "kettle-hole" shown in Fig. 1. This "kettle-hole" is bounded on the south by the end of the moraine lying east of the main basin which, ending abruptly with very steep sides, enclosed it on three sides, the north-eastern sector being only separated from the main basin by a narrow bridge rising about 1 ft. above the level of each basin. This bridge is of sandy clay covered with 2 or 3 in. (5 or 8 cm.) of peat and bears, like all the surrounding slopes, vegetation of the poplar Parkland.

The main basin and "kettle-hole" are illustrated in Pl. I, Phot. 2, Pl. II, Phot. 3, and the vegetation of the main basin may be described first.

Sphagnum-Andromeda association. This occupies an irregular area in the centre of the basin with several outliers of smaller extent. *Sphagnum* is dominant with *Andromeda polifolia* and *Rubus chamaemorus* subdominant. As accompanying plants, *Oxycoccus palustris* is frequent and *Menyanthes trifoliata* is present in the shallow depressions between the cushions of *Sphagnum*. A few of the older mounds are crowned with dwarf plants of *Betula glandulosa* and *Ledum latifolium*. These *Sphagnum* islands (the largest being about 125 m. in diameter) are bordered by a broad band of *Menyanthes*.

Caricetum association. This occupies the rest of the basin, and the vegetation, while differing slightly in the abundance of the accompanying plants in various regions, has the following composition:

| | | | |
|--|------|--|----|
| <i>Carex tenuiflora</i> Wahl. | d. | <i>Petasites sagittata</i> (Pursh) A. Gray | a. |
| <i>Juncus tenuis</i> Willd. | d. | <i>Betula glandulosa</i> Michx. | a. |
| <i>Glyceria nervata</i> (Willd.) Trin. | l.d. | <i>Salix balsamifera</i> Barr. | f. |
| <i>Rubus arcticus</i> L. | f. | <i>Eriophorum polystachyon</i> L. | f. |
| <i>Geum rivale</i> L. | f. | <i>Sagittaria graminea</i> Michx. | o. |
| <i>Potentilla palustris</i> Scop. | f. | <i>Scheuchzeria palustris</i> L. | o. |
| <i>Drosera rotundifolia</i> L. | f. | <i>Equisetum fluviatile</i> L. | r. |
| <i>Oxycoccus palustris</i> Pers. | l.a. | <i>Marchantia polymorpha</i> | r. |
| <i>Utricularia vulgaris</i> L. | a. | | |

Sphagnum is quite common over large areas, particularly towards the south end of the basin, forming a loose mat beneath the Carices.

Numerous pH determinations were made both in the *Sphagnum* islands and in the surrounding low-moor and these are given below.

On *Sphagnum* islands.

| | | | | |
|--|-----|-----|----|-----|
| <i>Sphagnum-Andromeda-Rubus</i> association | ... | ... | pH | 4.0 |
| Pool with <i>Andromeda</i> and <i>Hypnum</i> at margin of island | ... | ... | pH | 4.0 |
| Edge of small <i>Sphagnum</i> area with <i>Andromeda</i> | ... | ... | pH | 4.0 |
| <i>Sphagnum</i> patch among <i>Andromeda</i> , <i>Ledum</i> and <i>Oxycoccus palustris</i> | ... | ... | pH | 4.5 |

On *Caricetum*.

| | | | | |
|---|-----|-----|----|-----|
| Pool containing algae with <i>Hypnum</i> sp. | ... | ... | pH | 5.7 |
| Pool near bank with <i>Glyceria nervata</i> | ... | ... | pH | 5.8 |
| Pool containing <i>Hypnum</i> sp. | ... | ... | pH | 5.5 |
| Pool near edge of basin with <i>Carex</i> sp. | ... | ... | pH | 5.0 |

The earliest stage in the *Sphagnum* succession is the most acid, the acidity tends to decrease as *Ledum* makes its appearance, while all parts of the *Caricetum* show a diminished acidity.



Phot. 3. Small basin occupied by reed-swamp surrounded by moraine (p. 30).



Phot. 4. Centrifugal growth of *Sphagnum-Andromeda* association over *Caricetum* (p. 30).

Owing to the great number of pH determinations of different stages of the bog successions we have made over an area about 250 miles (400 km.) across, we are able to state generally that the several stages of high-moor successions are characterised by pH values varying within very small limits.

The general profile of this basin has been ascertained by borings and is illustrated in Fig. 1. The *Sphagnum-Andromeda* association here resembles the *Sphagnum-Andromeda* association bordering low-moors in the Nestow District (p. 38), but none of the later stages of the *Sphagnum* succession are represented here.

The surrounding region shows signs of having been burnt not once but many times, and the earlier successions have probably been influenced by fire. During the summer of 1926 there was never less than 8 inches (20 cm.) of water on the Caricetum, and in the earlier and later part of the season the ground was covered to a depth of 18 inches (46 cm.), and it may be doubted whether the area is ever dry enough for the peat to burn to any depth, although fire might spread through the aerial parts of the vegetation when withered in the autumn. Burning to this extent would not materially alter the course of succession. It would seem probable therefore that, in the absence of any indication that the topography has changed so as to produce permanent flooding, the present vegetation represents a primary succession. The sequence outwards of *Sphagnum-Andromeda*, *Carex-Hypnum-Betula*, *Carex-Hypnum-Salix*, with a border of *Glyceria nervata* at the margin of the basin, shows clearly that the growth is centripetal, and this is emphasised by the spread outwards of a sward of *Sphagnum* through the Caricetum, particularly at the south end of the basin.

The vegetation of the small depression or "kettle-hole" is, like many more such small depressions in this district, at the reed-swamp stage and was covered in September with about 2 feet (60 cm.) of water. The absence of the later stages of the low-moor succession and of muskeg raises the question why the successions have been so far delayed in small basins with steeply sloping sides. Topographical details show clearly that no change in the drainage of this basin has occurred. The unequal melting of the ice-sheet must have left many small lobes and then again many fragments partly or entirely buried. Such a mass embedded in a depression of this kind might remain unmelted for a long period of time and so delay the trend of events.

The Birch Bogs.

Although the lowlands are extensively occupied by bog forest they sometimes support vegetation at a more youthful stage. In some cases the apparently youthful stage of the vegetation is due to destruction or partial destruction of a bog forest by fire, but in other cases the succession is primary.

Birch moors are frequently due to the influence of burning. This has been pointed out by Cooper (4) in the forests of Isle Royale, where *Betula alba*

var. *papyrifera* when burnt, quickly grows up again from the roots, while the coniferous element in the association is destroyed. The same is true of *Betula glandulosa* and there are examples in this district where the bog, having been burnt at the *Larix-Betula* stage, results in the larch being killed and the original stage replaced by a moor occupied by birch, pine and *Hypnum*.

On the other hand, a very interesting and instructive case of a birch bog which is a primary association may be described from an area about a mile from the McLeod River. The bog covers an area about $2\frac{1}{2}$ miles (4 km.) long and varies greatly in width, averaging about $\frac{2}{3}$ of a mile (1 km.). It is bounded entirely by sand-hills of an average height of 20–50 feet (6–15 m.), whose sinuous course favours the development of many complex winding channels and bays running in from the main area of the bog. A preliminary traverse of the bog shows three main features: a central region of birch moor, a marginal region of muskeg of very irregular width, and a small lake about $\frac{1}{3}$ mile (0.5 km.) in diameter showing an interesting series of marginal successions.

A brief reference to the general features connected with this lake, which is shown in Pl. III, Phot. 5, may be given, as it shows a characteristic banding of vegetation round it and reproduces, in our opinion, the stages which succeeded one another in the earlier stages of development of the birch bog.

The depth of the lake is unknown, but shows about 7 in. (18 cm.) of clear water with a semi-liquid deposit below which was sounded to a depth of about 4 ft. (122 cm.). It contains a luxurious growth of *Hypnum wilsoni* Schimp. var. *hamatum* Lindb., *Potamogeton natans* L. and *Utricularia vulgaris* L. which are heavily encrusted with algae. The surface water of the lake is tenanted by *Nuphar advena* Ait.

The low-moor surrounding the lake consists of an association of the following plants:

| | | |
|--------------------------------|------|--|
| <i>Carex aquatilis</i> Wahl. | d. | <i>Tofieldia glutinosa</i> Michx. (Pers.) s. |
| <i>Carex diandra</i> Schrank. | c.d. | <i>Triglochin maritima</i> L. |
| <i>Carex paupercula</i> Michx. | f. | <i>Drosera longifolia</i> L. |
| <i>Hypnum</i> spp. | a. | <i>Salix</i> spp. |
| <i>Potentilla palustris</i> L. | s. | <i>Menyanthes trifoliata</i> L. |

with *Sphagnum acutifolium* var. *versicolor* Warnst. invading the outer margin from the surrounding muskeg. *Menyanthes* is particularly abundant near the lake, being rooted in the sedge mat and sending out horizontal rhizomes over the water as shown in Pl. III, Phot. 5.

Beyond this the ground rises slightly to a shelf of *Sphagnum* peat, the surface vegetation consisting of *Sphagnum*, *Ledum* and black spruce seedlings. To this young stage of the bog succession we apply the term *Ledum* moor. In this *Ledum* moor the following typical plants occur:

| | |
|-----------------------------------|---------------------------------|
| <i>Larix laricina</i> (seedlings) | <i>Potentilla palustris</i> L. |
| <i>Andromeda polifolia</i> L. | <i>Spiranthes</i> sp. |
| <i>Drosera rotundifolia</i> L. | <i>Eriophorum vaginatum</i> L. |
| <i>Oxycoccus palustris</i> Pers. | <i>Betula glandulosa</i> Michx. |

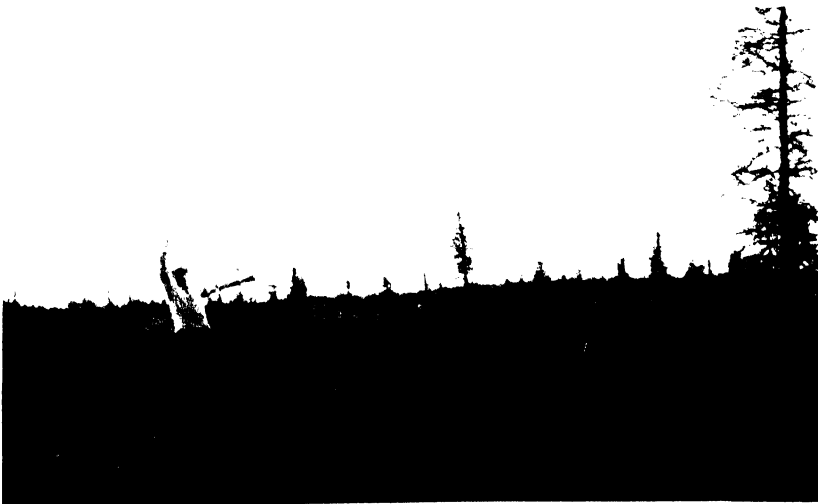
No evidence exists round this lake of the separation of larch moor and *Ledum* moor as described for lake No. 3.



Phot. 5. Lake with marginal banding of *Caricetum* and *Ledum* moor (p. 32).



Phot. 6. Birch-*Hylocomium* bog type (p. 33).



Phot. 7. Superficial roots of larch (p. 33).



Phot. 8. Fused roots of larch (p. 33).



Phot. 9. Superficial roots of larch with *Betula glandulosa* (p. 33).

Behind this ridge of muskeg we reach the flat birch moor that makes up the larger part of the bog. Owing to the recent draining of the area it has lately become comparatively dry.

The only trees on the moor are small larch, and of these for some reason, a large proportion is dead. The trees are sparsely distributed and most evenly spaced. They tend to grow in rows about 70 feet (21 m.) apart, the trees in the rows occurring at about every 6 feet (1.8 m.), so that they give the appearance of a carefully planted orchard. Their surface roots run over the swamp from one tree to another, forming a clearly visible net work, Pl. III, Phot. 7, Pl. IV, Phot. 9. The ridges formed by the roots support lines of *Betula glandulosa* along their length, which contrasts with the meadow-like depression between them, and marks out the moor into small compartments like the squares of a tennis court, Pl. III, Phot. 6. In a similar though much younger association near Lake Jolicoeur, described on p. 40, it was found that several individual seedling larch trees arose from one long root, no less than 11 seedlings about 1 ft. (30 cm.) high having developed at various points from a root 32 ft. (975 cm.) in length. The arrangement of the larch trees here suggested a similar feature and an endeavour was made to trace out the course in the mature trees. This proved very difficult owing to the finer roots breaking during the excavation; but the method of growth described above was not found in the young trees. We found, however, that the mature larch trees form a closely connected system. The numerous cases of root fusion that were observed suggests that here there is the possibility of a very interesting ecological relationship. A case of root fusion in two trees, one 40 years and the other 43 years old, standing 6 ft. 6 in. (2 m.) apart, is shown in Pl. IV, Phot. 8. This tendency to a raft-like root habit may be correlated with the needs of the trees in the saturated soil of their habitat.

The banks formed by the line of roots rise about 18 inches (46 cm.) above the intervening open spaces and may be due partly to the fact that the water level of the quaking bog has been lowered, and partly due to the more rapid growth and peat formation from the vegetation occupying the lines of larch roots. On account of greater aeration and drainage, they support a vegetation differing in many respects from that on the depressions between them. On the one hand is the shrub vegetation of the ridges, and on the other, the low areas, saturated or submerged, carpeted with moss and grasses.

The dominant plant of the ridges is *Betula glandulosa*, associated with which are:

| | | | |
|--------------------------------------|------|---------------------------------------|------|
| <i>Habenaria dilatata</i> Gray | f. | <i>Camptothecium nitens</i> Schimp. | f. |
| <i>Caltha palustris</i> L. | f. | <i>Cladonia fimbriata</i> (L.) Hoffm. | s. |
| <i>Parnassia palustris</i> L. | f. | <i>C. coccifera</i> (L.) Willd. | l.a. |
| <i>Rubus triflorus</i> Richards Raf. | a. | <i>Ledum latifolium</i> Ait. | v.r. |
| <i>Sarracenia purpurea</i> L. | l.a. | <i>Galium trifidum</i> L. | o. |

while such plants as *Rubus arcticus* L. and *Potentilla palustris* Scop., although found also on the depressions, grow much more luxuriantly on the ridges.

The ridges show some variation in flora in accordance with their aspect. When the ridges run east and west the moss tends to keep to the north side, and the birch to the south.

The dominant plant of the depressions is *Hypnum revolvens* Sw. which, at the period of the field work (August), was covered with a thick growth of an alga forming a dead black brittle covering over the mats of dessicated aquatic moss. The characteristic plants are as follows:

| | | | |
|---|----|---|----|
| <i>Hypnum revolvens</i> Sw. | d. | <i>Tofieldia glutinosa</i> (Michx.) Pers. | f. |
| <i>Muehlenbergia racemosa</i> (Michx.) B.S.P. | a. | <i>Epilobium densum</i> Raf. | o |
| <i>Rubus arcticus</i> L. | f. | <i>Carex</i> sp. | f. |
| <i>Caltha palustris</i> L. | a. | <i>Equisetum fluviatile</i> L. | o. |
| <i>Menyanthes trifoliata</i> L. | f. | <i>Antennaria</i> sp. | o. |
| <i>Stellaria crassifolia</i> Ehrh. | f. | <i>Aster junceus</i> Ait. | o. |

The water below the quaking mat of *Hypnum* has a pH of 6.0. Several borings were taken over the central region of this bog and no bottom was found at the limit of the boring apparatus which was 20 ft. (6.1 m.). Samples of peat were brought up from different depths. From 15 (4.6 m.) feet below the surface samples of peat showed the following plants:

| | |
|------------------------------------|--|
| <i>Chara</i> sp. fruits | <i>Hypnum revolvens</i> Sw. |
| <i>Scirpus</i> sp. fruits | <i>Hypnum</i> sp. |
| <i>Menyanthes trifoliata</i> seeds | <i>Larix laricina</i> —fragments of branches |

From a boring somewhat nearer the margin at a depth of 20 feet (6.1 m.) *Hypnum revolvens* Sw. was abundant, accompanying *Menyanthes trifoliata* and *Carex* spp.

These findings make it certain that this area has not passed through the high-moor stage and justify the conclusion that this area represents an early stage in the bog succession.

In every instance the sandhills which surround this bog are footed by a narrow zone of muskeg. Even sand moraines that stand up as islands near one margin of the moor are also fringed by muskeg, as though the zone consistently marked the shore line of an ancient lake.

Proceeding outwards from the centre of the moor, one first notices that the larch becomes more healthy and more thickly growing. The undergrowth is largely the ridge vegetation of the centre with the addition of invaders from the neighbouring muskegs, such as *Oxycoccus palustris*, *Polytrichum commune*, with *Sphagnum* and *Ledum*. Passing a transitional zone where black spruce seems to be invading the larch, we reach the muskeg itself, which is a stage in development of a young bog forest. The spruce is large and thickly growing and stands on a considerable depth of raw *Sphagnum* peat. The undergrowth is *Sphagnum magellanicum* Brid. and *Sphagnum acutifolium* var. *versicolor* Warnst. together with the typical ericaceous muskeg plants such as *Ledum latifolium* and *Vaccinium* sp.

This marginal arrangement of muskeg is illustrated in Fig. 2 and is very common elsewhere in the later stages of development. It is natural that muskeg, being a formation of the hydrarch series, should tend to surround lakes

and marshy places, and even when the lakes have disappeared or the swamps dried, the strips of bog forest mark their place along the foot of the surrounding hills.

As one ascends the sand-hill, the peat thins out, and while the trees themselves show no change except a greater luxuriance, the *Sphagnum-Ledum* undergrowth is replaced by a mat of *Hypnum*. This black spruce forest has a floor of a luxuriant growth of other mosses, such as *Hylocomium*, and an abundance of the lichen *Peltigera aphthosa* Willd. making up the climax association of the district.

Ascending further, we reach a transition belt in which young spruce are replacing the pine association of the sand-hills, while at the summit one usually finds the *Pinus contorta* association described above (Pl. II, Phot. 4).

These marginal zones are represented in Fig. 2.

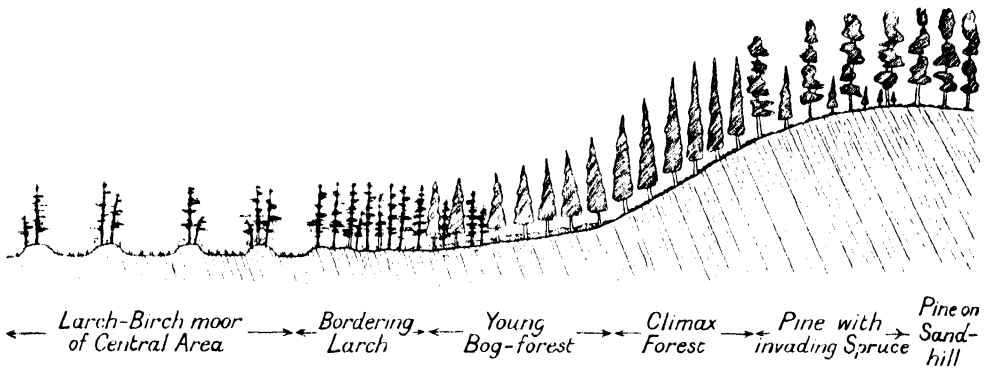


FIG. 2. Marginal zones of birch bog near McLeod River.

About a mile (1.6 km.) distant from the first moor, and in a similar position among sand-hills, there exists a smaller and drier moor. The striking similarity of the vegetation here shows it to be essentially of the same type of association as the first; but in this second area there are differences which we have reason to believe are subsequent developments, so that this is probably a later stage of the same hydrarch succession. This area therefore furnishes valuable evidence from which to construct the probable trend of events in bog succession in this district. The bog is clothed with a forest of very large larch and black spruce, and the undergrowth is more luxuriant than in the first moor, especially the birch, which is plentiful and grows to a height of about 4 feet (1.2 m.). Here the ridge vegetation is extensive and invades the depressions which are smaller and drier than in the first bog.

Vegetation belonging to a more mesophytic association is making its appearance. On the north side of the birch ridges *Sphagnum*, accompanied by *Andromeda*, is growing vigorously and spreading over old tree stumps. This, with the abundance of black spruce, heralds the transition from the birch to the *Ledum* moor.

The Bog Forests.

Only a small part of the lowlands is occupied by birch moor, the greater part being heavily forested. This forest consists of black spruce bog which is unlike the type described surrounding birch moor. It is not accompanied by an ericaceous undergrowth nor is it on a substratum of raw peat, but the undergrowth consists of *Hypnum* and broad-leaved mesophytes growing on decomposed black muck, these features marking it out as a distinct stage in the bog series. The thickly growing trees festooned with lichens surround small pools of dark water where grows a great depth of the delicate leaved moss *Hypnum cordifolium* Hedw. and *Caltha palustris*; while the tree roots that bound the pools are themselves felted with moss such as *Hypnum schreberi* Willd., *H. crista-castrensis* L. and *Hylocomium splendens* (L.) Schimp., Pl. V, Phot. 11.

The presence of the pools is probably due to the mosses not growing so readily immediately under the trees, leaving depressions about the tree roots which become filled with water. The banks of the pools are made higher by the fallen logs which lie criss-cross between the trees and become moss covered.

The chief shrubs found in the more open spaces are:

Ledum latifolium Ait.
Betula glandulosa Michx.
Salix spp.

Lonicera involucrata Banks
Ribes hudsonianum Richards
Alnus viridis V.C.

The most conspicuous grass of the forest is *Calamagrostis canadensis* (Michx.) Beauv., while *Carex aquatilis* Wahl. is abundant, Pl. V, Phot. 10.

The following herbaceous plants are also found amongst the mosses:

Microstylis ophioglossoides Nutt.
Epilobium angustifolium L.
Mitella nuda L.

Cornus canadensis L.
Caltha palustris L.
Potentilla palustris Scop.

This type of vegetation forms a continuous winding channel from Chip Lake to the McLeod River. Clearing may be so slight as to leave the characteristic pools unaffected, although hastening the invasion of sand-hill plants.

On the other hand, more extensive changes due to human interference, not only through logging but also through fire, produce extensive changes in the forest which may cause reversion to one of two secondary associations, either *Ledum* moor or low-moor. The reversion to *Ledum* moor by clearing is shown on each side of roads which pass through the bog forests. The same type of vegetation is also met with when the trees have been killed by burning. It was found that in both these cases the trees have been replaced by shrubs, the broad-leaved mesophytes by ericaceous xerophytes, and the mosses, *Hypnum* and *Hylocomium* by *Sphagnum*.

This very characteristic and definite association, the shrub stage of the muskeg, is most common in the more extensively cultivated country to the east, especially in the vicinity of Edmonton, while in the sparsely populated country to the west it is comparatively rare.



Phot. 10. Young stage of bog forest (p. 36).



Phot. 11. Mature bog forest with *Hyphnum* floor (p. 36).

The mature forests of the depressions may, when cleared, be even so far modified as to revert to low-moor.

In such cases the swampy forests that have been logged extensively usually show three types of ground vegetation:

(a) That which is antecedent to the clearing, such as *Hypnum cristacastrensis* L., *Sphagnum acutifolium*, *Menyanthes trifoliata*, and *Caltha palustris*. These are found in the more shaded parts.

(b) Vegetation belonging to the *Ledum* moor stage, e.g. *Ledum latifolium*, *Vagnera trifolia* and *Vaccinium vitis-idaea*.

(c) Vegetation in the more exposed situations, showing a reversion to the low-moor stage, of which the following is a representative list:

| | |
|---|---------------------------------|
| <i>Carex paupercula</i> Michx. | <i>Cladonia</i> sp. |
| <i>Calamagrostis canadensis</i> Michx. | <i>Andromeda polifolia</i> L. |
| <i>Muehlenbergia racemosa</i> (Michx.) B.S.P. | <i>Betula glandulosa</i> Michx. |
| <i>Rubus arcticus</i> L. | <i>Salix</i> spp. |

and in the damper places:

| | |
|-----------------------------------|---|
| <i>Equisetum fluviatile</i> L. | <i>Eriophorum</i> sp. |
| <i>Carex aquatilis</i> Wahl. | <i>Agrostis hyemalis</i> (Walt.) B.S.P. |
| <i>C. diandra</i> Schrank. | <i>Poa pratensis</i> L. |
| <i>Galium</i> sp. | <i>Epilobium</i> sp. |
| <i>Stellaria longifolia</i> Muhl. | <i>Cicuta bulbifera</i> L. |
| <i>Parnassia palustris</i> L. | <i>Aster juncus</i> Ait. |
| <i>Viola</i> sp. | <i>Carex leptalea</i> Wahl. |
| <i>Habenaria</i> sp. | <i>Carex gynocrates</i> Wormsk. |
| <i>Hypnum</i> spp. | |

THE NORTHERN FOREST.

General Considerations on Succession.

In certain extensive regions occur accumulations of sand in the form of hills 20–40 feet (6–12 m.) high. These great drifts probably represent the terminal moraine of either the main ice sheet or an extensive ice lobe towards the end of the last glaciation. The sand has probably been resorted by water and, no doubt, in the early days before the sand had become stabilised, wind also played a part in the formation of the hills.

Such sand regions are strictly localised in one sense, yet stretch in irregular bands over a considerable extent of country. There is usually an absence of foreign material in the sand. The longer axes of the hills are variable in direction and the general level of the summits suggests arrangement by water.

Such bands of sand-hills are often present in a district in which rock moraines abound, but rock moraines do not occur amongst the sand-hills.

A very marked feature is to be found in the development between the hills of perfectly flat basins of all sizes up to about half a kilometre across. In many cases one basin may lead into another by a curved channel, the difference in level between the two frequently being only two or three feet (60 to 90 cm.).

The region under discussion lies at the southern edge of the coniferous

forest in which some clearing and repeated burning has taken place. The northern forest is here represented by only one species *Pinus banksiana*, the other trees characteristic of this climatic formation being only met with farther north. This tree has an extensive distribution on the eastern side of the Rocky Mountains from Alaska to the region under discussion, and eastward to Labrador and Newfoundland, and just reaches south of the Great Lakes.

Large stretches of forest in which nearly every third tree of pine is badly infected by *Arceuthobium americana* Nutt. occurs south of the Athabasca Valley and this continues to the north-east of Battleford, Saskatchewan. The appearance of these forests is rendered remarkable by the numerous large broom-like outgrowths which often form the major part of the trees.

Unlike the Cordilleran region where *Picea mariana* invades sand-hills covered by the sub-climax of *Pinus contorta*, but few cases of invasion of *Pinus Banksiana* by black spruce have been observed, although muskegs covered with black spruce abut on the lower slopes of the sand-hills. The most characteristic plants of the undergrowth are *Alnus viridis*, *Arctostaphylos uva-ursi*, *Vaccinium canadense*, *Rubus strigosus*, *Rosa* spp., *Vaccinium vitis-idaea*, *Aster* spp., *Polytrichum juniperinum*, *Funaria hygrometrica*.

The flora and succession of associations on sand-hills will be described in future papers.

In regard to hydrarch successions, it may be stated that the district shows the following salient characteristics:

(a) The earlier stages of muskeg succession are well represented by the frequent association of marginal muskegs (high-moor) round central low-moor.

(b) Early stages of the birch bog are present.

(c) Many of the muskegs occupying small basins are at a later stage than those in the Parkland belt.

(d) Low-moors resulting from burning of muskegs are common in the district.

These features may now be described from representative selected areas.

(a) *Marginal muskegs round low-moor.* The Nestow district is 55 miles (88 km.) north of Edmonton and within the northern forest. It is a region of sand-hills which form a band about 15 miles (24 km.) from north to south. The flat basins between the hills are occupied either by muskegs at a stage of *Ledum* moor or by low-moors characterised by marginal muskegs.

One typical basin may be described first. It is oval in shape, extending about $\frac{1}{4}$ mile (0.4 km.) north to south, and is bounded on the west by an abrupt rise, while the east side is flanked by a gently rising hill. The main basin is occupied by low-moor, while the east margin is bounded by muskeg, which, as one passes from the low-moor to the sand-hill, shows a series of distinct bands, the relationships of which are illustrated in Fig. 3. The low-moor consists of the following:



Phot. 12. *Andromeda* moor (p. 39).

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| | | | |
|--|------|-----------------------------------|----|
| <i>Carex paupercula</i> Michx. | d. | <i>Betula glandulosa</i> Michx. | s. |
| <i>Eriophorum angustifolium</i> Roth. | s.d. | <i>Triglochin maritima</i> L. | s. |
| <i>Salix pedicellaris hypoglauca</i> Fern. | s.d. | <i>Potentilla palustris</i> Scop. | s. |
| <i>Hypnum</i> sp. | a. | <i>Menyanthes trifoliata</i> L. | s. |
| <i>Equisetum fluviatile</i> L. | s. | | |

Towards the east side of the basin *Sphagnum* forms a close growth on the ground, between the taller vegetation, and extends out continuously from the marginal muskeg. Peat less than 1 ft. (30 cm.) below the surface of this low-moor contains no *Sphagnum*, but consists entirely of the remains of *Carices*, *Menyanthes* and *Eriophorum*, hence the *Sphagnum* is of recent occurrence.

On the east margin the vegetation changes abruptly and gives place to four bands representing successive stages of muskeg succession.

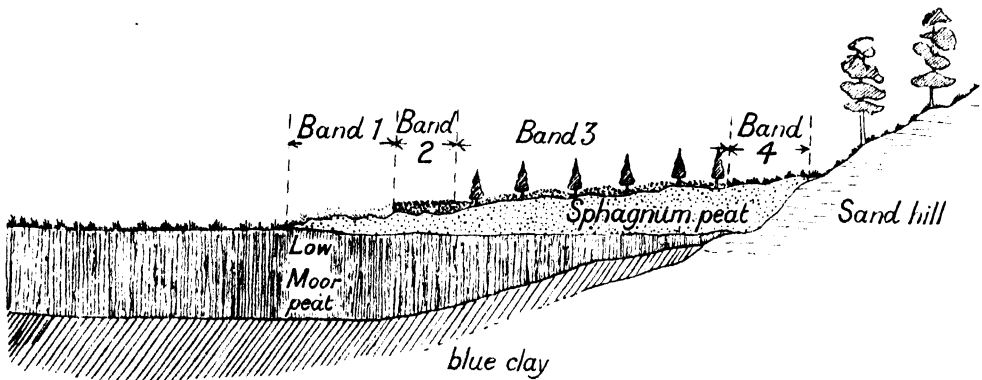


FIG. 3. Marginal high-moor with banding of vegetation surrounding low-moor with *Sphagnum* growth. Nestow area.

Band 1. Represents the earliest stage and consists of *Sphagnum-Andromeda* association:

| | | |
|------------------------------------|--|--|
| <i>Sphagnum acutifolium</i> Ehrh. | d. | |
| <i>Andromeda polifolia</i> L. | d. | |
| <i>Eriophorum vaginatum</i> L. | r. | |
| <i>Betula glandulosa</i> Michx. | a few scattered seedlings | |
| <i>Oxycoccus palustris</i> Pers. | r. | |
| <i>Scheuchzeria palustris</i> L. | r. | |
| <i>Rubus chamaemorus</i> L. | invading a few scattered patches chiefly on the outer margin | |
| <i>Ledum latifolium</i> Ait. | a few isolated plants | |
| <i>Picea mariana</i> (Mill) B.S.P. | a few seedlings 6 inches (15 cm.) high. | |

This band is 39 ft. (11.9 m.) wide and rises somewhat abruptly from the low-moor. The vegetation is shown in Pl. VI, Phot. 12.

Band 2:

| | | | |
|---------------------------------|----|--------------------------------------|--------------------------|
| <i>Sphagnum</i> spp. | d. | <i>Vagnera trifolia</i> L. | |
| <i>Ledum latifolium</i> Ait. | d. | <i>Eriophorum vaginatum</i> | 1. (a few small patches) |
| <i>Vaccinium vitis-idaea</i> L. | a. | <i>Cladonia pyxidata</i> (L.) Hoffm. | l.a. |
| <i>Rubus chamaemorus</i> L. | a. | <i>C. rangiferina</i> (L.) Web. | l.a. |
| <i>Andromeda polifolia</i> L. | r. | <i>Oxycoccus palustris</i> Pers. | r. |

Picea mariana is scarce and scattered but is more frequent than in Band 1. This association forms a band 20 ft. (6.1 m.) in width and is illustrated by Pl. VII, Phot. 13. It is essentially *Ledum* moor, as described elsewhere in this

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paper, except for the presence of a few plants of *Andromeda* still lingering on from the earlier stages of Band 1.

Band 3:

| | | | |
|------------------------------------|----|----------------------------------|----|
| <i>Picea mariana</i> (Mill) B.S.P. | d. | <i>Vaccinium vitis-idaea</i> L. | f. |
| <i>Ledum latifolium</i> Ait. | d. | <i>Oxycoccus palustris</i> Pers. | r. |
| <i>Sphagnum acutifolium</i> Ehrh. | f. | | |

This band constitutes the young bog forest stage and represents the most mature stage in the bog succession that we have yet met with in the northern coniferous forest. The band is 104 ft. (31.7 m.) wide.

Band 4. This is a transitional band, 20 ft. (6.1 m.) wide, passing directly into the slope of the sand-hill so that a good deal of sand has drifted into the peat. The vegetation consists of:

| | | | |
|---------------------------------------|----|---------------------------------|----|
| <i>Vaccinium canadense</i> Kalm. | d. | <i>P. commune</i> L. | o. |
| <i>Ledum latifolium</i> Ait. | d. | <i>Vaccinium vitis-idaea</i> L. | r. |
| <i>Polytrichum juniperinum</i> Willd. | o. | <i>Equisetum sylvaticum</i> L. | o. |

The sand-hill bordering on this series of bands of muskeg types has the following flora:

| | | | |
|--|----|---|----|
| <i>Pinus banksiana</i> Lamb. | d. | <i>Carex houghtonii</i> Torr. | f. |
| <i>Arctostaphylos uva-ursi</i> Spreng. | a. | <i>Oryzopsis pungens</i> (Torr.) Hitch. | f. |
| <i>Vaccinium canadense</i> Kalm. | a. | <i>Agrostis hiemalis</i> (Walt.) B.S.P. | f. |
| <i>V. vitis-idaea</i> L. | o. | <i>Festuca ovina</i> L. | f. |
| <i>Rubus strigosus</i> Michx. | o. | <i>Erigeron glabellus</i> Nutt. | f. |
| <i>Rosa</i> spp. | f. | <i>Artemisia caudata</i> Michx. | f. |
| <i>Alnus viridis</i> D.C. | a. | <i>Campanula rotundifolia</i> L. | f. |
| <i>Polytrichum juniperinum</i> Willd. | f. | | |

This area is typical of many of these low-moor basins amongst the sand-hills, although in some cases the banding is not so complete; stages may be telescoped and, again, the marginal muskegs may be altered by fire.

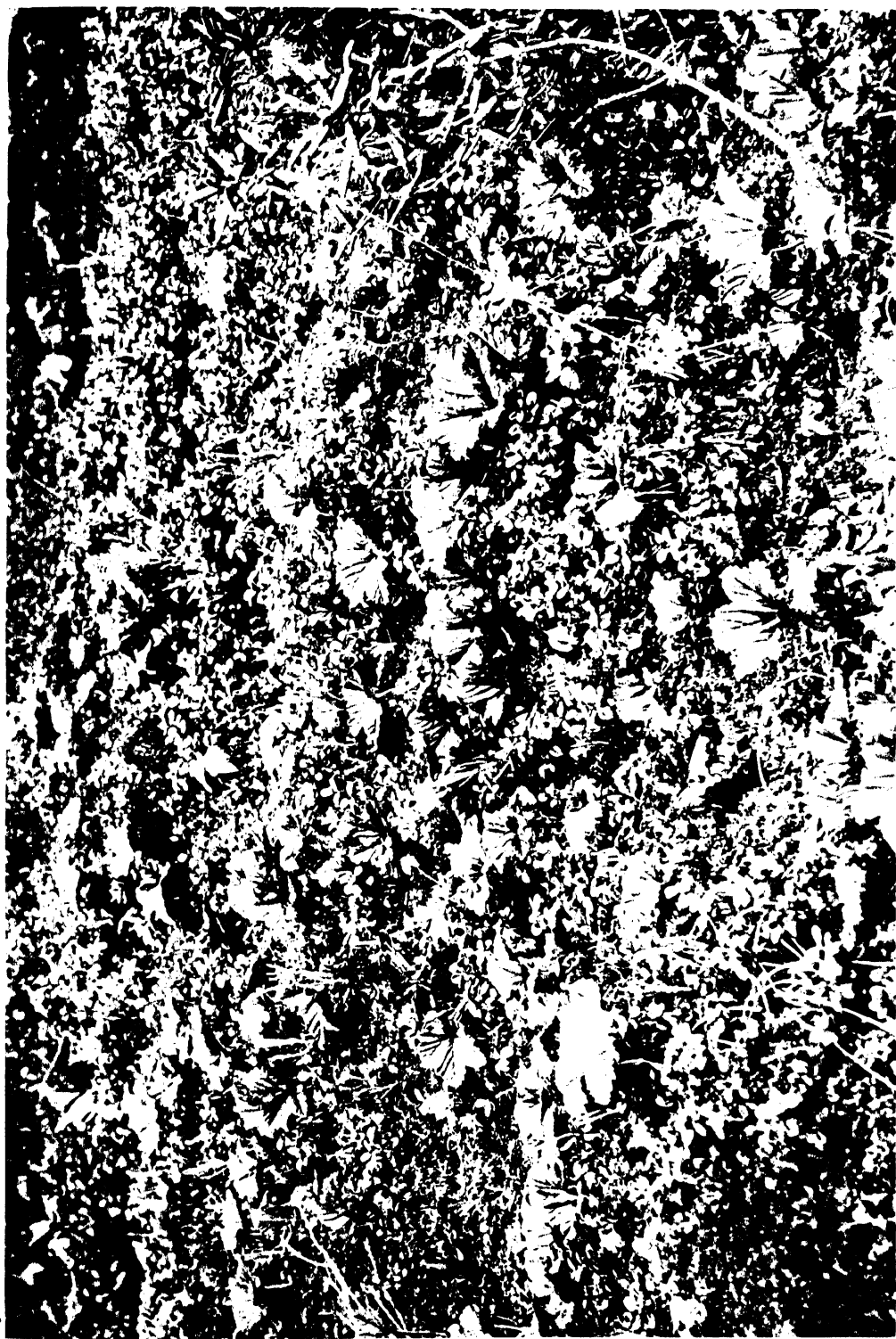
In some examples the basin has been covered with high-moor, subsequently burnt, with partial regeneration of the high-moor at the margin as described on p. 42. In many cases the burning in the central area has been partial and has left relics of the old pre-burn high-moor as small irregular islands now scattered over the low-moor. In these cases regeneration always appears to be centripetal, the high-moor successions spreading in from the margin.

(b) *Early stages of the birch bog.* About 20 miles (32 km.) within the northern forest on the Edmonton-Athabasca trail lies Jolicoeur Lake. The northern shores are bounded by successive bands of low-moor, birch moor, and larch-spruce muskeg and the stages of vegetation here are similar to the McLeod bog described on p. 32. The low-moor bordering the lake has a flora consisting of

| | | | |
|---------------------------------|----|--------------------------------|----|
| <i>Carex diandra</i> Schrank. | d. | <i>Triglochin maritima</i> L. | a. |
| <i>Menyanthes trifoliata</i> L. | a. | <i>Equisetum fluviatile</i> L. | a. |
| <i>Caltha palustris</i> L. | o. | <i>Salix</i> sp. | r. |

The *Larch-Birch-Hypnum* moor bears a striking resemblance to the McLeod bog, the association consisting of the following:

| | | | |
|--------------------------------------|----|--|----|
| <i>Larix laricina</i> (Du Roi) Hoch. | d. | <i>Spiranthes</i> sp. | f. |
| <i>Betula glandulosa</i> Michx. | d. | <i>Eriophorum callitrix</i> Cham. | f. |
| <i>Hypnum revolvens</i> Sw. | d. | <i>Tofieldia glutinosa</i> (Michx.) Pers. | a. |
| <i>Menyanthes trifoliata</i> L. | f. | <i>Equisetum fluviatile</i> L. | a. |
| <i>Salix</i> sp. | f. | <i>Muehlenbergia racemosa</i> (Michx.) B.S.P. | f. |



Phot. 13. *Rhizus-Ficinia* moor. N. 300.

The individual trees of larch tend to assume linear arrangement with long roots running near the surface. The birch shrubs occur chiefly on the slightly raised ridges above the larch roots. What is most striking about this bog is the less mature stage of the association as compared with the McLeod bog. The larch trees are merely seedlings, the *Hypnum* mat of the depressions is saturated with water and consists of a loose luxuriantly growing carpet as contrasted with the dried crust of moss in the McLeod bog. As in the McLeod bog (p. 32), this birch bog is bordered with *Ledum* moor.

(c) *Mature muskegs*. The latest successions observed are exemplified by two small areas near Red Water River on the border line of the Parkland and northern forest about 50 miles (80 km.) north of Edmonton. They occur on the slopes of sand-hills and adjacent to low-moors. The first example is a small area not more than a hundred metres in extent on the slope of a sand-hill bordering a low-moor. Numerous mounds of peat composed of *Sphagnum* occur, but the living moss is being smothered by the abundant growth of *Ledum latifolium*. The vegetation consists of the following:

| | | |
|------------------------------|-----|---|
| <i>Picea mariana</i> | ... | Close growth of old trees |
| <i>P. albertiana</i> | ... | Small trees and seedlings spreading in |
| <i>Ledum latifolium</i> | ... | Still dominant |
| <i>Sphagnum</i> spp. | ... | Scarce and rare in small patches on the north side of mounds |
| <i>Vaccinium vitis-idaea</i> | | Very common and tending to cover the mounds of <i>Sphagnum</i> peat |
| <i>Ribes</i> sp. | ... | Abundant |
| <i>Cladonia pyxidata</i> | | |
| <i>Equisetum sylvaticum</i> | | Common. |

Great wastage of peat is occurring over the bare areas, and the original muskeg vegetation appears to be destined to be replaced by white spruce.

The second example is in the same district and occupies a similar position but is at a much later stage. Here, again, *Picea mariana* forms a close canopy on the muskeg; *Sphagnum* is absent although mounds of peat formed from *Sphagnum* are frequent. These mounds and the channels between are occupied with stunted *Ledum* much of which is dying or dead, with a mixed flora consisting of *Anemone dichotoma* L., *Equisetum sylvaticum*, *Salix* sp. and in the more open spots seedlings of *Populus tremuloides* and *Picea albertiana*. These two areas at slightly different stages are instructive as showing the complete disappearance of the *Sphagnum-Ledum-Picea mariana* association and its replacement by a mixed vegetation with the tendency to a cover of white spruce rather than black spruce.

Although the cases described above represent a late succession in the high-moor series, no forest climax comparable to the western region has yet been observed, although such an ultimate stage may exist farther north. The two cases given do suggest a climax of white spruce, a type which we consider to occur also in the muskegs of the Parkland, although there, owing to the action of various factors to be discussed later, the sub-climax of *Ledum* moor appears to persist.

(d) *Low-moors resulting from burning*. Other depressions among the sand-

hills are occupied mainly by low-moor, but these usually show remnants of *Ledum* moor. The presence of charring in the peat and sometimes of burnt timber suggest why the basins are not covered with high-moor. Return to high-moor is indicated by the occurrence of thin carpets of fresh *Sphagnum* over the floors of some of these moors. Various features in connection with the invasion and re-establishment of *Sphagnum* are illustrated by the three moors described in detail below. Apparently, *Hypnum* is the first moss to become established, a stage illustrated by low-moor No. 1; here, there is no sign of invasion by *Sphagnum*, even though old mounds of this moss occur towards the border. In other cases, *Sphagnum* has succeeded *Hypnum*, forming a thin mat over the greater part of the moor (low-moor No. 2), or is spreading in from bordering remnants of old muskeg (low-moor No. 3). The dominant sedges of these moors are *Carex lasiocarpa* and *C. paupercula*.

Low-moor No. 1. This moor is about 3 acres (1.2 hectares) in area and is surrounded by sand-hills from which most of the pines have been burned off. In isolated parts of the moor, there are a few remnants of trees, whilst towards the border there are occasional remnants of *Sphagnum* mounds occupied by *Ledum*, *Vaccinium vitis-idaea*, *Rubus arcticus* and other plants. The peaty material which forms the floor of the basin is decidedly charred to a depth of 6 inches (15 cm.) or more. The moor is dominated by *Hypnum* sp. (Harpidioid type) and *Carex paupercula* Michx. with which are associated:

| | | | |
|--|------|--|----|
| <i>Salix pedicellaris</i> hypoglauca Fern. | s.d. | <i>Equisetum fluviatile</i> L. | a. |
| <i>Potentilla palustris</i> (L.) Scop. | f. | <i>Spiranthes romanzoffiana</i> Coult. | o. |
| <i>Menyanthes trifoliata</i> L. | f. | <i>Triglochin maritima</i> L. | o. |
| <i>Eriophorum</i> sp. | f. | | |

Low-moor No. 2. This moor covers a lobed depression and is separated from another moor (low-moor No. 3) by a sand-bar, Fig. 4. Most of the pines on the surrounding sand-hills have been destroyed by fire. At the base of the hills and immediately adjoining the low-moor there is a copious growth of *Vaccinium canadense* and *Ledum*.

The west lobe of the moor has a narrow grass border, consisting of *Calamagrostis canadensis* (d.), *Agrostis hiemalis* (f.), *Spiranthes romanzoffiana* (o.), and *Salix* (o.). The central part is dominated by *Sphagnum* and carices. In places, however, *Sphagnum* is dead or considerably dried up, while a Harpidioid *Hypnum* is abundant locally. *Sphagnum* remains cover the floor to a depth of about 4 inches (10 cm.). Below the *Sphagnum* there is a layer of *Hypnum-Eriophorum* peat, which in turn is underlaid by *Carex-Eriophorum* peat. The most prominent carices of the present vegetation are *Carex lasiocarpa* Ehrh., *Carex utriculata* Boott., *Carex paupercula* Michx., and *Eriophorum chamissonis* C. A. Mey., these being either abundant throughout or locally dominant. Accompanying plants are *Carex canescens* L. and *Potentilla palustris*.

The east lobe of the moor is drier than the west lobe and has a broad border dominated by *Calamagrostis canadensis*, and *Agrostis hyemalis*, with which is associated *Juncus dudleyi* Wieg. in the driest places. The small central part

is a *Caricetum*, consisting of the following: *Carex lasiocarpa* (d.), *Eriophorum* (f.), *Potentilla palustris* (s.), *Carex aquatilis* (o.), *Sphagnum* (forming a thin, desiccated layer).

Low-moor No. 3. This moor resembles No. 2, except for the occurrence of *Sphagnum-Ledum* mounds. As shown in Fig. 4, these mounds occur mainly on the west side adjoining the sand-bank. Extending inwards from these older mounds are fresh *Sphagnum* mounds, which in the central part of the moor are followed by a thin layer of the moss. On the east side of the moor there is a close mat of a Harpidioid *Hypnum*, but very little *Sphagnum*. The dominant sedges of the moor are *Carex paupercula* and *C. lasiocarpa*.

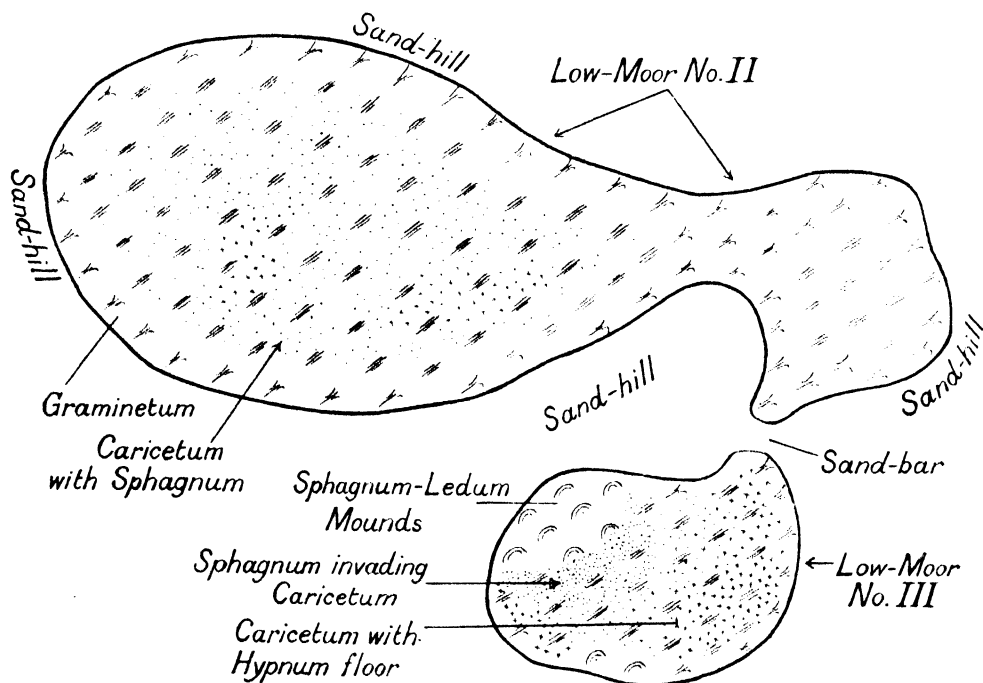


FIG. 4. Showing relation of vegetation over low-moors II and III, Nestow district.

THE PARKLAND AREA.

In a previous paper (1) a general account of the topography and vegetation of the Parkland was given, followed by a description of typical muskegs. During the field work of 1926 particular attention was given to reed-swamps and low-moors of the Parkland and secondary successions in muskegs due to burning. Many of the depressions in the region investigated are occupied in part by small lakes, which, in western Canada, are known as "sloughs." Most of these sloughs are bordered by reed-swamp, which is surrounded in turn by low-moor and Parkland vegetation. Many basins have been extensively invaded and filled up, with the result that they are now completely covered with vegetation essentially of the low-moor type. The vegetation of various depressions may be described below, under the following headings:

I. Reed-swamps and low-moors of the Parkland.

- (a) Reed-swamps and low-moors associated with sloughs and lakes.
- (b) Low-moors occupying very wet basins.
- (c) Low-moors occupying comparatively dry basins.

II. Retrogressive changes in muskegs due to burning.

- (a) General account of retrogression and subsequent successions.
- (b) Vegetation of low-moors formed by retrogressive changes.

I. Reed-swamps and Low-moors of the Parkland.

(a) *Reed-swamps and low-moors associated with sloughs and lakes.* The vegetation adjoining the majority of sloughs and lakes in the region investigated consists of two types namely, reed-swamp and low-moor, these terms being used in Warming's sense (5). Reed-swamp occurs next to the water and is surrounded by low-moor, the two types frequently merging to a considerable extent, being at times scarcely distinguishable. This is illustrated by Area No. V described below.

Naturally these reed-swamps and low-moors present many ecological problems that can be solved only by critical studies extending over a number of years. At the present time, a description will be given of the vegetation of certain typical areas (Nos. I to VI, pp. 46-51), leaving for future investigation various problems concerning succession, ecological equivalents and the influence of burning, grazing, mowing and of fluctuations in water-level.

The more important features illustrated by the areas described below may be summarised as follows:

- (1) Reed-swamp vegetation is characterised by the following dominants:

Scirpus validus Vahl.
Typha latifolia L.
Sparganium sp.

Eleocharis palustris (L.) R. & S.
Carex atherodes Spreng.
Scolochloa festuacea (Willd.) Link.

The latter is dominant in broad bands adjoining many of the larger sloughs and lakes (Area No. IV), and certain large, though shallow, sloughs in the Cooking Lake region are almost entirely covered with a close stand of this grass.

Reed-swamp species of less general occurrence, but locally abundant, include the following:

Acorus calamus L. (Area No. VI)
Calla palustris L. (Area II and V)
Phragmites communis Trin. (not present in any of the
 areas described, but abundant in certain places)
Beckmannia erucaeformis (L.) Host.
Hippuris vulgaris L.

(2) Reed-swamp associations of larger sloughs and lakes are two in number, namely *Scirpus-Typha* and *Scolochloa-Carex atherodes* associations, the first being usually an open community, standing in several inches of water, and the second a closed community surrounding the first (e.g. Area No. I, larger

slough, and Area No. IV). An exception to this statement is provided by Lily Lake (Area No. V), whose marginal vegetation consists in the main, of *Scirpus*, *Typha* and *Sparganium*, whilst *Scolochloa* and *Carex atherodes* are absent.

Reed-swamp vegetation of smaller sloughs is variable in composition, commonly consisting of isolated communities dominated by such species as *Scirpus validus*, *Scolochloa festuacea*, *Sparganium* sp. and *Eleocharis palustris*, as is illustrated by Areas II, III and VI.

(3) Low-moor vegetation is characterised by the following dominants, as shown in Areas I, III and IV.

Glyceria grandis Wats.
Glyceria pulchella Nash
Carex aquatilis Wahl.
Carex utriculata Boott.

Poa palustris L.
Calamagrostis americana Scribn.¹
Calamagrostis canadensis (Michx.) Beauv.
Salix spp.

Species of less general occurrence, but locally abundant, include

Carex pseudo-cyperus L. (Area No. II)
Carex diandra Schrank.

C. lasiocarpa Ehrh.

Drier portions of low-moors that have been frequently mown are often dominated by *Poa pratensis* L. (Areas III and VI), or less commonly by *Juncus ater* Rydb. (Area No. IV).

(4) Several low-moor associations have been recognised, the salient types being as follows:

Glyceria-Carex association, adjoining reed-swamp (Area No. I, larger slough).

Carex aquatilis-C. utriculata association, adjoining reed-swamp (Area No. I, smaller slough) — the absence of *Glyceria* here being probably due to lowering of the water-level in summer and to trampling by cattle.

Calamagrostis americana association, occupying drier parts than the preceding associations (Area No. III).

Poa palustris association, occupying habitats similar to the last (Areas III and VI).

Calamagrostis americana-Poa palustris association (Area No. IV).

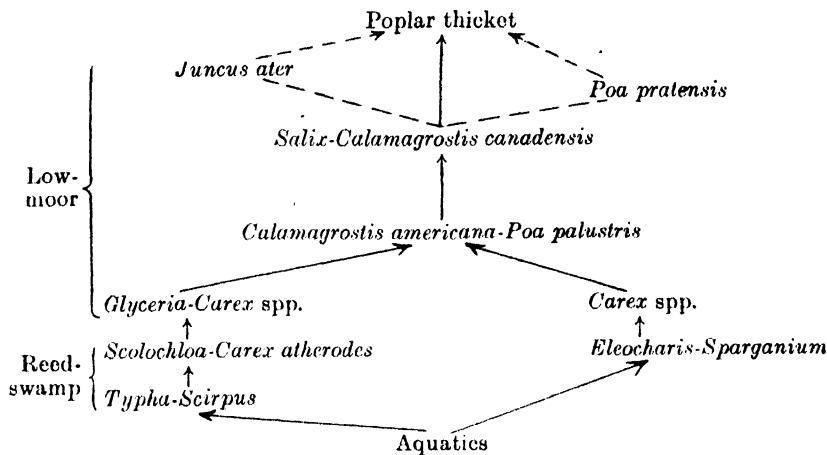
Salix-Calamagrostis canadensis association, which occupies the outer and less wet parts of low-moors, in the absence of mowing, burning and heavy grazing (Area No. III).

(5) Probable successions of associations adjoining sloughs are indicated in connection with the detailed descriptions of Areas I, II and III. The following composite scheme incorporates our tentative conclusions concerning hydrarch successions of the more important reed-swamp and low-moor associations. The associations dominated by *Poa pratensis* and *Juncus ater* occur on hay-meadows and are largely due to the influence of mowing.

¹ There is some uncertainty regarding the specific name of the grass which throughout this paper is referred to as *Calamagrostis americana* Scribn.

Area No. I. This area is located 18 miles (29 km.) south-east of Edmonton; and is approximately 1500 by 400 feet (450 by 120 m.) in size. The depression in which it lies contains two sloughs, the larger of which is shown in Plate VIII, Phot. 14. These sloughs are bordered by reed-swamp merging into low-moor, which is backed by the poplar association of the adjoining morainic ridges. The pH of the water in the reed-swamp part of the larger slough is 6.5.

The floating vegetation of the larger slough consists mainly of *Lemna minor* L., which, by the middle of the summer, covers a considerable part of the slough. *Lemna* is also abundant in the smaller slough, where it is accompanied by *Ricciocarpus natans* (L.) Corda.



The reed-swamp of the larger slough contains two more or less distinct associations: (1) *Scirpus-Typha* association consisting of clumps of *Scirpus validus* and *Typha latifolia*, interspersed with a small amount of *Scolochloa*, *Sparganium* and *Carex atherodes*.

(2) *Scolochloa-Carex* association, dominated by *Scolochloa festucacea* and *Carex atherodes*, and forming a continuous and very dense band of vegetation, about 50 feet (15 m.) in width, round the slough. In the early summer this association has the general appearance of a *Caricetum*, but later, the sedge becomes overtopped and obscured by *Scolochloa*, and the association takes on the aspect of a *Graminetum*. This association is shown in Plate VIII, Phot. 14, as a conspicuous, light-coloured band. The photograph was taken in the middle of July, at a time when the pale, greenish-yellow inflorescences of *Scolochloa* were quite prominent. Accompanying plants of this association are:

| | | | |
|----------------------------------|-----|-------------------------------|----|
| <i>Sagittaria arifolia</i> Nutt. | a. | <i>Scirpus validus</i> Wahl. | s. |
| <i>Sparganium</i> sp. | f. | <i>Carex aquatilis</i> Wahl. | s. |
| <i>Carex utriculata</i> Boott. | la. | <i>Glyceria grandis</i> Wats. | s. |

The rhizomes of *Scolochloa* and other plants of the association form a floating mat, which, in most places, is sufficiently firm to support one's weight.

The reed-swamp vegetation of the smaller slough is dominated by *Scolochloa* and *Eleocharis palustris*, the latter being dominant in numerous large patches

in the outer part. Accompanying plants include *Scirpus validus* (f.), *Sparganium* sp. (a.) and *Sagittaria* sp.

The low-moor vegetation adjoining the larger slough consists of two associations.

(1) *Glyceria-Carex* association, in which *Glyceria grandis* is dominant, and the two sedges, *Carex aquatilis* Wahl. and *C. utriculata* Boott., subdominant. The accompanying plants include:

| | | | |
|---|------|------------------------------------|----|
| <i>Hippuris vulgaris</i> L. | l.a. | <i>Aster puniceus</i> L. | f. |
| <i>Alopecurus aristulatus</i> Michx. | l.a. | <i>Galium trifidum</i> L. | f. |
| <i>Calamagrostis</i> sp. | l.a. | <i>Bidens cernua</i> L. | f. |
| <i>Agrostis hiemalis</i> (Walt.) B.S.P. | l.a. | <i>Scutellaria galericulata</i> L. | s. |
| <i>Sparganium</i> sp. | f. | <i>Sium cicutaefolium</i> Schrank. | s. |
| <i>Sagittaria arifolia</i> Nutt. | f. | <i>Cicuta maculata</i> L. | o. |
| <i>Rumex persicarioides</i> L. | f. | <i>Polygonum</i> sp. | o. |
| <i>Ranunculus scleratus</i> L. | f. | | |

In July, this association takes on a reddish-brown colour due to the inflorescences of *Glyceria*, and stands out in sharp contrast with the lighter coloured band of *Scolochloa* (Plate VIII, Phot. 14).

(2) *Calamagrostis-Salix* association, dominated by *Calamagrostis* sp., and *Salix* spp. This association has been grazed and trampled by cattle, and consequently, is not the product of undisturbed nature. In the wetter parts, small plants of *Salix* are abundant, while shrubs and small trees of *Salix* form isolated clumps and groves. In the drier parts, *Salix* is scattered and the grass is very closely grazed. Among the accompanying plants of the association are:

| | |
|-------------------------------|-----------------------------------|
| <i>Parnassia palustris</i> L. | <i>Erigeron philadelphicus</i> L. |
| <i>Fragaria</i> sp. | <i>Stellaria longifolia</i> Muhl. |
| <i>Rubus arcticus</i> L. | <i>Taraxacum officinale</i> Weber |
| <i>Potentilla</i> sp. | |

The low-moor adjoining the smaller slough differs from that of the larger slough in the absence of *Glyceria*, the association next to the reed-swamp being dominated by *Carex aquatilis* and *C. utriculata*. A probable explanation of this circumstance lies in the fact that the water-level of the smaller slough falls very considerably at times during the summer, whilst that of the larger slough fluctuates to a lesser degree. The frequent lowering of the water-level may, in itself, prevent the establishment of *Glyceria* around the smaller slough; or, trampling and grazing of cattle during the dry periods may be of greater importance as limiting factors in this connection. There is considerable evidence that the two common sedges of the low-moor are able to withstand wider variations in water-supply and also greater damage on the part of cattle than can *Glyceria*.

Obviously, the sloughs of this basin are being gradually invaded and filled up by vegetation. The succession of associations in the case of the larger slough appears to be as follows: *Typha-Scirpus* → *Scolochloa-Carex atherodes* → *Glyceria-Carex* spp. → *Calamagrostis-Salix* → Poplar thicket. The succession in the case of the smaller slough seems to be thus: *Scolochloa-Eleocharis-Sparganium* → *Carex* spp. → *Calamagrostis-Salix* → Poplar thicket.

Area No. II. This basin-like area occurs in the same locality as No. I, and is about 500 feet (150 m.) in diameter. The reed-swamp vegetation surrounding the central slough of the basin consists of the following plants:

| | | | |
|--|------|---|------|
| <i>Eleocharis palustris</i> (L.) R. & S. | l.a. | <i>Scolochloa festucacea</i> (Willd.) Link. | a. |
| <i>Typha latifolia</i> L. | l.a. | <i>Calla palustris</i> L. | l.a. |
| <i>Sagittaria</i> sp. | a. | | |

This is surrounded by low-moor—a *Caricetum*, in which two associations may be distinguished.

(1) *Carex pseudo-cyperus* association, forming a definite narrow band and dominated by *Carex pseudo-cyperus* L. This sedge has thus far been met with in only one other place, namely adjoining another lake in the same general district; here, the sedge forms a narrow fringe next to the water round the lake and is backed by muskeg of the young bog forest type.

(2) *Carex aquatilis* association, constituting a broad band (about 30 metres in width) and dominated by *Carex aquatilis*, accompanied by an abundance of *Glyceria*, together with scattered plants of a few other species. *Calamagrostis* is frequent to subdominant in the outer, somewhat drier parts of the *Caricetum*. This association extends to the adjoining moraines, where there is quite a sharp transition to Parkland vegetation.

The vegetational sequence in this basin is apparently as follows: *Eleocharis-Scolochloa-Sagittaria*→*Carex pseudo-cyperus*→*Carex aquatilis-Glyceria*→*Calamagrostis* (invasion only beginning).

Area No. III. This area, located in the Cooking Lake district, is irregular in shape and is flanked by low moraines. It contains three small ponds or sloughs, the largest of which is shown in Plate VIII, Phot. 15. These sloughs support a luxuriant growth of *Lemna*, and are bordered by small clumps of reed-swamp vegetation composed of *Typha latifolia*, *Scirpus validus* and *Scolochloa festucacea*. One small and very wet place in the area is dominated by *Scolochloa*, another by *Carex atherodes* and still another by a mixture of *Scolochloa*, *Carex atherodes* and *Beckmannia erucaeformis*.

Adjoining these wetter parts of the area are broad stretches of low-moor vegetation, in which the following associations may be distinguished:

(1) *Carex aquatilis* association, occupying places that are quite wet in the spring, and dominated by *Carex aquatilis*, with which are associated:

| | | | |
|------------------------------------|----|------------------------------------|----|
| <i>Carex utriculata</i> Boott. | a. | <i>Galium trifidum</i> L. | f. |
| <i>Stellaria crassifolia</i> Ehrh. | f. | <i>Sium cicutaefolium</i> Schrank. | f. |
| <i>Scutellaria galericulata</i> L. | f. | <i>Cicuta maculata</i> L. | o. |
| <i>Stachys scopulorum</i> Greene | f. | | |

(2) *Calamagrostis* association, occupying somewhat drier parts than the last, and consisting of the following plants:

| | | | |
|---|------|--------------------------------|----|
| <i>Calamagrostis americana</i> Scribn. | d. | <i>Mentha</i> sp. | f. |
| <i>Carex aquatilis</i> Wahl. | l.a. | <i>Cicuta maculata</i> L. | f. |
| <i>Calamagrostis canadensis</i> (Michx.) Beauv. | l.a. | <i>Aster salicifolius</i> Ait. | f. |
| <i>Stellaria longifolia</i> Muhl. | f. | <i>Aster puniceus</i> L. | o. |
| <i>Scutellaria galericulata</i> L. | f. | | |



Phot. 14. Reed-swamp and low-moor adjoining a slough. Area No. I (p. 46).



Phot. 15. Marginal vegetation of small slough. Area No. III (p. 48).



Phot. 16. Lily lake showing *Nuphar* and portion of the reed swamp. Area No. V (p. 50).

This association is bordered by the Parkland vegetation of the moraines, by association No. 3 or by association No. 4.

(3) *Salix-Calamagrostis canadensis* association, a narrow band bordering association No. 2 in certain places, and dominated by *Salix* spp. and *Calamagrostis canadensis*. This association merges with the Poplar association of the moraines.

(4) *Poa palustris* association, which, in certain places, adjoins association No. 2, and which occupies extensive and rather dry portions of the low-moor. It consists of the following plants:

| | | | |
|-----------------------------------|--------------|---|----|
| <i>Poa palustris</i> L. | d. | <i>Potentilla</i> sp. | s. |
| <i>Poa pratensis</i> L. | s.d. | <i>Stachys scopulorum</i> Greene | s. |
| <i>Phalaris arundinacea</i> L. | l.d. or l.a. | <i>Vicia americana</i> Muhl. | s. |
| <i>Hordeum jubatum</i> L. | f. | <i>Stellaria longifolia</i> Muhl. | s. |
| <i>Phleum pratense</i> L. | l.a. | <i>Anemone canadensis</i> L. | s. |
| <i>Fragaria</i> sp. | f. | <i>Sisyrinchium</i> sp. | s. |
| <i>Achillea</i> sp. | f. | <i>Calamagrostis canadensis</i> (Michx.) Beauv. | s. |
| <i>Taraxacum officinale</i> Weber | f. | <i>Salix</i> spp. | s. |
| <i>Erigeron philadelphicus</i> L. | s. | | |

Mowing and burning have been important factors in the development of these associations. The drier portions of the low-moor have been regularly mown for a considerable number of years and the peripheral parts of the hay-meadows have been repeatedly burned. Only where mowing and burning have not occurred or have been infrequent does the *Salix-Calamagrostis canadensis* association develop. Elsewhere, either association No. 2 or association No. 4 adjoins the morainal vegetation. A natural succession of associations in the low-moor appears to be as follows: *Carex-aquatilis* → *Calamagrostis americana* → *Salix-Calamagrostis canadensis* → Poplar thicket. In the drier sections of the area, *Poa palustris* would almost certainly have a place in the natural sequence, either as a distinct association or as a prominent constituent of a *Calamagrostis* association. This conclusion is supported by evidence from other areas.

Area No. IV. This area is typical of those associated with Cooking Lake and the larger sloughs in the district. It adjoins a short arm of Cooking Lake and is flanked by low banks. The pH of the water in the arm is 8. Proceeding from the water's edge to the adjoining banks, there is a gentle rise in level and a gradation of vegetation from the strictly aquatic to rather dry grassland. The low-moor part of the area has been mown many times.

The vegetation next to the water is reed-swamp, and this merges gradually into low-moor. In the reed-swamp, the following bands of vegetation occur:

(1) An inner band consisting of *Lemna* (a.), *Scirpus validus* (a.) and *Typha latifolia* (l.a.).

(2) A mixed band in which the following species are scattered or locally dominant: *Carex atherodes*, *Scolochloa festucacea*, *Alopecurus aristulatus*, *Eleocharis palustris*.

(3) A dense stand of *Scolochloa* (in flower by July 10). The straw of this grass has formed a thick layer over the underlying quaking mat.

(4) A second band of *Scolochloa* (not yet in flower by July 10).

(5) A mixed band, consisting of *Scolochloa* (a.):

| | | | |
|--------------------------------------|-------------|--|------|
| <i>Carex atherodes</i> Spreng. | a. and l.d. | <i>Phalaris arundinacea</i> L. | l.a. |
| <i>Poa palustris</i> L. | a. | <i>Calamagrostis americana</i> Scribn. | f. |
| <i>Urtica gracilis</i> Ait. | a. | <i>Epilobium adenocaulon</i> Hauskn. | f. |
| <i>Ranunculus sceleratus</i> L. | a. | <i>Senecio palustris</i> L. | f. |
| <i>Alopecurus aristulatus</i> Michx. | l.d. | | |

The low-moor consists of the following more or less distinct bands:

(1) A somewhat wet band, dominated by *Alopecurus aristulatus* and *Poa palustris*, with which are associated:

| | | | |
|--|----|-------------------------------------|----|
| <i>Carex atherodes</i> Spreng. | a. | <i>Hordeum jubatum</i> L. | f. |
| <i>Calamagrostis americana</i> Scribn. | a. | <i>Sium cicutaeifolium</i> Schrank. | f. |
| <i>Urtica gracilis</i> Ait. | a. | <i>Viola palustris</i> L. | f. |
| <i>Stellaria</i> sp. | a. | <i>Geum macrophyllum</i> Willd. | f. |

(2) A drier band, dominated by *Poa palustris* and *Calamagrostis americana* Scribn. with which are associated:

| | | | |
|-----------------------------------|------|-----------------------------------|----|
| <i>Hordeum jubatum</i> L. | f. | <i>Stellaria longifolia</i> Muhl. | s. |
| <i>Taraxacum officinale</i> Weber | f. | <i>Erigeron philadelphicus</i> L. | s. |
| <i>Viola</i> sp. | l.a. | <i>Phleum pratense</i> L. | s. |

(3) An outer, narrow, intermittent band, dominated by *Juncus ater* Rydb.

The low-moor vegetation is bordered by the *Salix-Cornus-Populus* thicket of the adjoining banks, or (where a road skirts the bank) by a flora including:

| | |
|-----------------------------------|-------------------------------|
| <i>Carex douglasii</i> Boott. | <i>Potentilla anserina</i> L. |
| <i>Taraxacum officinale</i> Weber | <i>Phleum pratense</i> L. |
| <i>Plantago major</i> L. | |

The mixed nature of the flora of this area, particularly of the reed-swamp, is probably correlated with the fact that the water level of the lake has fluctuated considerably during recent years.

Area No. V. This area adjoins the north end of Lily Lake, which is located beside the old Athabasca trail, about 35 miles (56 km.) north of Edmonton. The lake is approximately $\frac{1}{4}$ by $1\frac{1}{2}$ miles (0.4 by 2.4 km.) in size, and lies in a narrow valley which extends in either direction from the lake for a few miles. Lily Lake is fittingly named, because in midsummer it is literally covered with the yellow water-lily, *Nuphar advena* Ait., Plate VIII, Phot. 16. Among other aquatics in the lake are *Lemna*, *Potamogeton* and numerous Algae. The water of the lake is very alkaline, the pH of a sample taken near the shore being about 10.

The lake is bordered at the north end by a fringe of vegetation composed mainly of *Typha latifolia* and *Sparganium* sp. while *Scirpus validus*, *Glyceria* sp. and *Carex aquatilis* are locally abundant. Closely adjoining this marginal association is a narrow Caricetum composed chiefly of *Carex diandra* Schrank. and *C. lasiocarpa* Ehrh. The mat formed by these sedges is quaking but fairly dry on top and quite firm. Outside of this band there is a spongy marshy area, which is occupied by a mixed flora, as follows;

| | | | |
|--|------|------------------------------------|----|
| <i>Menyanthes trifoliata</i> L. | c.d. | <i>Scutellaria galericulata</i> L. | f. |
| <i>Carex diandra</i> Schrank. | c.d. | <i>Triglochin maritima</i> L. | f. |
| <i>Calla palustris</i> L. | l.a. | <i>Parnassia palustris</i> L. | f. |
| <i>Calamagrostis</i> sp. | l.a. | <i>Galium trifidum</i> L. | f. |
| <i>Potentilla palustris</i> (L.) Scop. | l.a. | <i>Sium cicutaefolium</i> Schrank. | s. |
| <i>Eriophorum</i> sp. | l.a. | <i>Aster junceus</i> Ait. | s. |

Extending up the valley from the marshy area just described there is a Caricetum several hundred metres in length and bounded on either side by *Salix-Alnus-Populus* thicket. The Caricetum consists mainly of the following species:

| | | | |
|---|------|---|------|
| <i>Carex aquatilis</i> Wahl. | d. | <i>Calamagrostis</i> sp. | f. |
| <i>Carex diandra</i> Schrank. | l.d. | <i>Mentha canadensis</i> L. var. <i>glabrata</i> Benth. | l.d. |
| <i>Parnassia palustris</i> L. | a. | <i>Stellaria longifolia</i> Muhl. | f. |
| <i>Scutellaria galericulata</i> L. | a. | <i>Stellaria crassifolia</i> Ehrh. | s. |
| <i>Carex utriculata</i> Boott. | l.a. | <i>Aster puniceus</i> L. | s. |
| <i>Agrostis hiemalis</i> (Walt.) B.S.P. | l.a. | <i>Aster junceus</i> Ait. | s. |
| <i>Bromus ciliatus</i> L. | l.a. | <i>Habenaria</i> sp. | s. |
| <i>Caltha palustris</i> L. | l.a. | <i>Salix</i> spp. | s. |
| <i>Rubus triflorus</i> Richards | l.a. | <i>Betula glandulosa</i> Michx. | s. |
| <i>Rubus arcticus</i> L. | l.a. | <i>Poa pratensis</i> L. | s. |
| <i>Potentilla palustris</i> (L.) Scop. | l.a. | <i>Ranunculus macounii</i> Britt. | s. |
| <i>Poa palustris</i> L. | f. | | |

Two additional species, namely, *Eleocharis acicularis* (L.) R. & S. and *Juncus nodosus* L. are locally abundant on a trail through the area. In parts of the Caricetum, some of the grasses are more frequent than is indicated by the frequencies of the above list, whilst elsewhere, willows are very abundant.

Farther along the valley there is an area of denuded muskeg and burned conifers, whilst in a large arm of the valley on the west side, there is unburnt muskeg. Most of the denuded area is occupied by carices, grasses and other plants similar to those listed above. An additional species, abundant in this area, is *Equisetum fluviatile* L.

Beyond the region of denuded muskeg, there is another Caricetum of the type described above. This is followed by a series of Saliceta and Gramineta, extending over a distance of about 2 miles (3.2 km.). Included also in this section of the valley are two small sloughs. The vegetation adjoining one of these sloughs will now be described as Area No. VI.

Area No. VI. As explained above, this area adjoins a small slough (about 120 metres in diameter) in the Lily Lake valley. The vegetation surrounding the slough consists of the following associations, the first two of which may be regarded as reed-swamp.

(1) An inner band, occurring in the water near the periphery of the slough, and in which *Eleocharis palustris*, *Hippuris vulgaris* and *Sparganium* sp. are co-dominants.

(2) A narrow band, in which *Acorus calamus*, *Scolochloa festucacea* and *Carex utriculata* are co-dominants, while *Scirpus validus* and *Typha latifolia* are locally dominant.

(3) A band about 30 ft. (9 m.) in width constituted as follows:

| | | | |
|---|------|------------------------------------|----|
| <i>Glyceria grandis</i> Wats. | a. | <i>Stellaria crassifolia</i> Ehrh. | f. |
| <i>Calamagrostis americana</i> Scribn. | a. | <i>Cicuta bulbifera</i> L. | f. |
| <i>Alopecurus aristulatus</i> Michx. | l.a. | <i>Cicuta maculata</i> L. | s. |
| <i>Galium trifidum</i> L. | f. | <i>Rumex persicarioides</i> L. | o. |
| <i>Mentha canadensis</i> L. var. <i>glabrata</i> Benth. | f. | | |

(4) An outer, broad band, about 500 ft. (150 m.) in width, dominated in most parts by *Poa palustris*. Accompanying plants include

| | |
|--|---|
| <i>Poa pratensis</i> L. | (dominant in large patches, especially in the outer, drier parts of the moor) |
| <i>Hordeum jubatum</i> L. | a. |
| <i>Phleum pratense</i> L. | f. |
| <i>Agrostis hiemalis</i> (Walt.) B.S.P. | f. |
| <i>Geum</i> sp. | s. |
| <i>Senecio flavovirens</i> Rydb. var. <i>thomsoniensis</i> Greenm. | s. |
| <i>Arnica chamissonis</i> Less. | s. |

This Graminetum, like almost all of those investigated, has been regularly mown for a considerable number of years.

(b) *Low-moors occupying very wet basins*. These moors are of particular interest because they represent stages in the filling up of wet basins by carices, *Hypnum* and other plants, and, because they occur in basins very similar to those occupied by muskeg. Why muskeg has not developed in the depressions under consideration is not apparent; probably, a more thorough investigation of low-moors such as Nos. IX and X (described below) and of neighbouring muskegs will throw light on this question.

Among low-moors occurring in very wet basins, two types have been recognised, viz.:

(1) Those characterised by a central Caricetum, standing in water throughout the summer and containing *Utricularia vulgaris* as a subdominant plant. This type is illustrated by Areas VII and VIII, moors occurring in widely separated districts and very dissimilar in size. Of considerable interest is the fact that the floor of Area No. VII is covered with a mat of *Hypnum*. This moss occurs also in the underlying peat, but only in the uppermost layer, indicating that *Hypnum* has invaded the area in comparatively recent times. There is some evidence that moors of this type may through time develop floating mats of vegetation similar to those of the second type.

(2) Those characterised by a large, central, quaking mat, consisting mainly of *Hypnum* (species of the section Harpidium), *Menyanthes* and carices, the most abundant sedge being *Carex paupercula*. This type is illustrated by Areas IX and X, the former being of particular interest, because of the occurrence, in the *Hypnum* mat, of two small colonies of *Sphagnum*.

Area No. VII. This moor occurs about 50 miles (80 km.) west of Edmonton, in the transitional belt between Parkland and Cordilleran forest. It is a large low-moor, measuring approximately 400 by 1100 ft. (120 by 335 m.), and is surrounded by low moraines with gently sloping sides. The area is really a shallow lake, which is covered, however, with a dense vegetation, in which carices are most prominent. Even in very dry seasons, the water is 4 to 12

inches (10 to 30 cm.) in depth over most of the area. The pH of the water is about 6 near the periphery, and about 6.5 in the central part of the moor.

The moor rests upon a bed of peat varying in depth from 18 inches (46 cm.), in the outer region, to 22 inches (56 cm.) in the central part. Identifiable remains in the peat are mainly fruits, seeds and cuticles of carices. In the uppermost part of the peat there is also a considerable amount of *Hypnum*. Below the peat there is a thin layer of black clay ("muck"), and underlying the latter is a gray, sandy clay, on which an analysis is given on p. 67.

The banks adjoining the moor are, in the main, occupied by poplar-willow thickets, willows being particularly abundant near the margin of the moor. Associated with the willows are various mosses (including *Aulacomnium palustre* (L.) Schwaegr., and:

| | |
|---|--------------------------------|
| <i>Rubus triflorus</i> Richards | <i>Pirola</i> sp. |
| <i>Lysimachia thyrsiflora</i> L. | <i>Viola</i> sp. |
| <i>Scutellaria galericulata</i> L. | <i>Habenaria</i> sp. |
| <i>Agrostis hiemalis</i> (Walt.) B.S.P. | <i>Glyceria pulchella</i> Nash |
| <i>Stellaria longifolia</i> Muhl. | |

The floor of the moor is covered in most places with a dense mat, consisting of *Hypnum sendtneri* Schimp. (probably accompanied by other harpidioid Hypna) and *Utricularia vulgaris* L. A third immersed species, namely, *Potamogeton americanus* C. & S., is abundant in peripheral parts of the moor. Apparently, *Hypnum* has invaded the area in comparatively recent times, because this moss occurs only in a thin, upper stratum of the peat. In small, isolated parts of the moor, the submerged vegetational mat is buoyed up to some extent and is sufficiently firm to support one's weight.

The rooted vegetation of the moor consists of two main parts, viz.:

(1) An outer Graminetum, varying in width from 20 to 50 ft. (6 to 15 m.), and dominated by *Glyceria pulchella*. Accompanying plants include *Potamogeton americanus*, *Lysimachia thyrsiflora* and *Eriophorum Chamissonis*.

(2) A large, central Caricetum, occupying over three-fourths of the moor, and composed of the following:

| | | | |
|--|-------------|--|------|
| <i>Carex lasiocarpa</i> Ehrh. | a. and l.d. | <i>Carex paupercula</i> Michx. | l.a. |
| <i>Carex diandra</i> Schrank. | a. and l.d. | <i>Carex bebbii</i> Olney | l.a. |
| <i>Carex utriculata</i> Boott. | a. and l.d. | <i>Potentilla palustris</i> (L.) Scop. | a. |
| <i>Eriophorum chamissonis</i> C. A. Mey. | a. and l.d. | <i>Triglochin maritima</i> L. | f. |
| <i>Carex canescens</i> L. | f. | <i>Potamogeton americanus</i> C. & S. | l.a. |
| <i>Carex chondrorrhiza</i> Ehrh. | l.a. | <i>Equisetum fluviatile</i> L. | s. |
| <i>Carex aquatilis</i> Wahl. | l.a. | <i>Salix</i> sp. | o. |

Area No. VIII. This is a very small, circular low-moor, being only about 40 ft. (12 m.) broad, situated in a pot-hole depression in a morainic region near Cooking Lake (Plate IX, Phot. 17). Like low-moor No. VII, it is very wet and is covered with a dense stand of sedge vegetation, in which *Utricularia vulgaris* is a prominent submerged plant. Mosses, however, do not accompany *Utricularia* in this case. The water of the basin is about 1 foot (30 cm.) in depth in midsummer and has a pH value of approximately 6.

The vegetation of the moor consists of two associations, viz.:

(1) An outer, narrow Graminetum, dominated by *Calamagrostis canadensis*, with which are associated *Glyceria* sp. (l.a.) and *Potentilla palustris* (f.). This association merges on the outside with the poplar thicket of the surrounding moraine, and on the inside passes abruptly to the central Caricetum. There is a sharp drop in the floor of the basin at the boundary between Graminetum and Caricetum.

(2) A central Caricetum, in which *Carex utriculata* is dominant, *Utricularia vulgaris* subdominant, *Potentilla palustris* frequent, and *Ranunculus sceleratus* locally abundant.

Area No. IX. This moor occupies a small basin, about 150 ft. (45 m. in diameter (Plate IX, Phot. 18), and occurs in the immediate vicinity of No. VIII. Like the latter, it holds a considerable quantity of water, the pH of which is about 6. It differs markedly from No. VIII, however, in having a central quaking mat, on which Carices, *Menyanthes* and a harpidioid *Hypnum* are prominent. Below the quaking mat, there is *Carex-Hypnum* peat (mainly liquid peat) to a depth of about 4 ft. (120 cm.). Beneath the Caricetum, there is firmer peat, 3½ ft. (105 cm.) in thickness. The peat of the basin is underlain by a bluish, sandy clay.

Adjoining this low-moor, and on a somewhat higher level, is another low-moor (in the main, a semi-dry Caricetum), and connecting with the latter is a small, dry muskeg with a broad border dominated by carices. It is probable that water may at times overflow from the muskeg and adjoining low-moor into Area No. IX.

The vegetation of Area No. IX consists of three rather well defined associations, the first two of which form concentric bands round the third.

(1) A narrow, peripheral Graminetum, consisting of *Calamagrostis canadensis* (d.), *Carex aquatilis* (f.), *Glyceria pulchella* (s.) and *Petasites* sp. (o.).

(2) A Caricetum, about 30 ft. (9 m.) in width, consisting of *Carex aquatilis* (d.), *Carex utriculata* (l.s.d.) and *Potentilla palustris* (f.).

(3) A *Carex-Menyanthes-Hypnum* association, occupying a central quaking mat, and composed of *Carex paupercula* (c.d.), *Menyanthes trifoliata* (c.d.), *Hypnum vernicosum* Lindb. (c.d.), (possibly accompanied by other harpidioid Hypna), *Carex chordorrhiza* (s.d.), *Carex diandra* (l.d.), *Potentilla palustris* (a.), *Eriophorum chamissonis* (l.a.), *Salix* sp. (l.a.), (small shoots about 30 cms. in height), *Scutellaria galericulata* (o.), *Cicuta maculata* (o.), and *Sphagnum* sp. (l.d.), the latter forming two small low mounds.

The occurrence of vigorous colonies of *Sphagnum* in the quaking mat suggests the possibility that this moss might in time encroach upon the surrounding vegetation and dominate the central part of the moor. Whereas the water of the moor in general, and likewise water held by the *Hypnum*, has a pH of 6, that squeezed out of the *Sphagnum* gave a pH of 4, whilst the pH of a sample taken about 2 inches from the periphery of a *Sphagnum* patch was 5.8. It is plainly evident, therefore, that *Sphagnum* acidifies water which it holds.



Phot. 17. A small wet pot-hole depression with a bordering *Graminetum* and central *Caricetum*. Area No. VIII (p. 53).



Phot. 18. A very wet basin with a central quaking mat of *Hypnum-Menyanthes*. Area No. IV (p. 54).

Area No. X. This moor, Plate X, Phot. 19, has been referred to in an earlier paper (1) in connection with a description of Muskeg No. I. The basins that contain Muskeg No. I and the low-moor now under consideration are separated only by a moraine and are seemingly very similar in their topography. Why low-moor has developed in one basin and high-moor in the other basin is not clearly evident at the present time, although a possible explanation is given below.

Compared with No. IX, this moor is somewhat drier in midsummer, contains no *Sphagnum*, has a greater variety of carices and other plants, but otherwise is very similar. The pH of the water throughout the moor is about 5.8.

The peat in the central part of the moor is about 3 ft. (90 cm.) thick and rests upon a sticky, blue clay. To a depth somewhat exceeding 30 cm., the peat contains *Hypnum revolvens* Sw., *H. sendtneri* Schimp. and *Meesia longiseta* Hedgw., and also remains of *Menyanthes* and various carices. The lower strata of the peat contain seeds and other remains of a number of species, including *Potamogeton*, but no *Hypnum* or other mosses. At a depth of about 2 ft. (60 cm.) in the peat a considerable amount of beaver-gnawed wood was encountered. Evidence of this kind suggests the possibility that the beaver may have played an important part in connection with vegetational development in the basin, perhaps by temporarily blocking the outlet of the basin with a dam, thus increasing the depth of water, and consequently delaying the establishment of marsh and moor plants in the central part of the basin. Possibly, therefore, this basin contained a deep slough at a time when prevailing climatic conditions were particularly favourable for the development of high-moor in marshy habitats, and during the period when *Sphagnum* became established in the adjoining basin (Muskeg No. I).

The vegetation of the moor consists of three associations, arranged in concentric fashion, and constituted as follows:

(1) A narrow, peripheral Graminetum, composed of:

| | | | |
|--|------|---|----|
| <i>Glyceria pulchella</i> Nash | d. | <i>Potentilla palustris</i> (L.) Scop. | f. |
| <i>Eleocharis palustris</i> (L.) R. & S. | l.a. | <i>Calamagrostis</i> sp. | o. |
| <i>Alopecurus aristulatus</i> Michx. | l.a. | <i>Glyceria borealis</i> (Nash) Barcheld. | o. |

(2) A broad Caricetum, consisting of:

| | | | |
|--|------|------------------------------------|----|
| <i>Carex utriculata</i> Boott. | l.d. | <i>Carex chordorrhiza</i> Ehrh. | a. |
| <i>Carex diandra</i> Schrank. | l.d. | <i>Sium cicutaefolium</i> Schrank. | a. |
| <i>Eleocharis palustris</i> (L.) R. & S. | l.d. | <i>Sparganium</i> sp. | s. |
| <i>Carex atherodes</i> Spreng. | l.d. | <i>Salix</i> sp. | s. |
| <i>Glyceria pulchella</i> Nash | a. | <i>Rumex</i> sp. | o. |
| <i>Potentilla palustris</i> (L.) Scop. | a. | | |

(3) A central, quaking mat, much drier on the surface than the Caricetum, and dominated by the following plants:

| | |
|--|--------------------------------|
| <i>Hypnum aduncum</i> Hedw. (and probably other harpidioid Hypna) | <i>Carex paupercula</i> Michx. |
| <i>Menyanthes trifoliata</i> L. | <i>Carex diandra</i> Schrank. |

Other species include:

| | | | |
|---------------------------------|------|-----------------------------|------|
| Potentilla palustris (L.) Scop. | a. | Viola mackloskeyi Lloyd | l.a. |
| Carex canescens L. | l.d. | Galium trifidum L. | f. |
| Eriophorum angustifolium Roth. | l.a. | Scutellaria galericulata L. | s. |

(c) *Low-moors occupying comparatively dry basins.* Moors of this type occupy the shallower and drier depressions of the region investigated. In general they are covered with water in spring and early summer, but become comparatively dry later in the growing season. The vegetation of the moors consists mainly of carices, willows and grasses, the latter being dominant on drier moors that have been regularly burned, mowed or grazed.

Certain of these areas were at one time occupied by muskeg, retrogression to low-moor being a consequence of drainage and burning (*vide* Area XIII, p. 62). This conclusion is based upon information obtained from early settlers and upon an examination of Area XIII and other areas similar in character. Many of the moors under consideration, however, have undoubtedly arisen by the filling up of shallow sloughs, the aquatic stage having been followed by carices, and the latter by willows and grasses in many cases.

The peat of the moors varies from 1 to 3 ft. (30 to 90 cm.) in thickness and rests upon a floor of blue clay. The upper strata of the peat consists mainly of cuticles and seeds of carices, sometimes accompanied by remains of *Hypnum*, whilst the lower stratum of the peat commonly contains seeds of *Potamogeton* and other aquatics.

Among these moors three main types may be recognised, namely, Cariceta, Saliceta and Gramineta. In general, Cariceta occupy the wetter depressions and gradually change to Saliceta as the depressions become drier, whilst Saliceta usually develop into poplar thicket upon further drying. In addition to willows, Saliceta contain a number of other species, of which *Calamagrostis canadensis* (Michx.) Beauv. is frequently abundant. As a consequence of burning, grazing and mowing, many Saliceta have been changed to Gramineta. The latter are, therefore, artificial communities created by human interference; when left undisturbed for a short period of time, they revert to Saliceta, or, if conditions have become quite dry, they are succeeded by Poplar thicket.

(1) *Cariceta.* The vegetation of many of these moors resembles that of a very wet Caricetum already described (p. 52), differing, however, in the absence of *Potamogeton*, *Utricularia* and frequently of *Hypnum*. Many of the wetter Cariceta are dominated by *Carex aquatilis* Wahl. whilst the somewhat drier ones are usually dominated either by *C. utriculata* Boott. or by *C. diandra* Schrank. Certain small and very wet moors, among the moraines of the Cooking Lake region, are dominated by *Carex atherodes* Spreng., a sedge which occurs more commonly in a reed-swamp association (p. 44).

A more detailed description of the vegetation of Cariceta may be given by reference to a particular depression, which is composed of three main parts, as follows:

(i) A very wet part, containing water to a depth of about 30 cm., except in the driest seasons, and occupied by the following species:

| | | | |
|--------------------------------|------|--|----|
| <i>Carex aquatilis</i> Wahl. | d. | <i>Potentilla palustris</i> (L.) Scop. | f. |
| <i>Carex diandra</i> Schrank. | a. | <i>Triglochin maritimum</i> L. | s. |
| <i>Equisetum fluviatile</i> L. | a. | <i>Eriophorum</i> sp. | s. |
| <i>Carex utriculata</i> Boott. | l.a. | <i>Rumex</i> sp. | o. |

(ii) A somewhat drier part, containing about 30 cm. of water in early summer, but dry on the surface later, and occupied by the following plants:

| | | | |
|--|------|---|------|
| <i>Carex diandra</i> Schrank. | d. | <i>Menyanthes trifoliata</i> L. | l.a. |
| <i>Equisetum fluviatile</i> L. | s.d. | <i>Carex stipata</i> Muhl. | l.a. |
| <i>Potentilla palustris</i> (L.) Scop. | a. | <i>Triglochin maritima</i> L. | s. |
| <i>Carex aquatilis</i> Wahl. | l.a. | <i>Eriophorum</i> sp. | s. |
| <i>Poa palustris</i> L. | l.a. | <i>Hypnum</i> (forming a thin mat in places). | |
| <i>Glyceria pulchella</i> Nash | l.a. | | |

(iii) A much drier part than the last, dry on the surface except in spring and during periods of heavy rainfall, and supporting the following vegetation:

| | | | |
|---|------|---|------|
| <i>Carex diandra</i> Schrank. | c.d. | <i>Potentilla palustris</i> (L.) Scop. | f. |
| <i>Poa palustris</i> L. | c.d. | <i>Stellaria</i> spp. | f. |
| <i>Equisetum fluviatile</i> L. | a. | <i>Parnassia palustris</i> L. | l.a. |
| <i>Rubus arcticus</i> L. | a. | <i>Agrostis hiemalis</i> (Walt.) B.S.P. | l.a. |
| <i>Salix</i> spp. (small plants abundant) | | <i>Betula glandulosa</i> Michx. | s. |

(2) *Saliceta*. As already stated, *Saliceta* contain besides willows a number of other species, of which *Calamagrostis canadensis* is commonly abundant; indeed, this grass is frequently subdominant or even co-dominant. Among the willows and other plants that occur in *Saliceta* are the following:

| | | | |
|---|--|--|--|
| <i>Salix petiolaris</i> J. E. Smith | | <i>Carex prairea</i> Dewey | |
| <i>Salix planifolia</i> Ph. | | <i>Carex praegracilis</i> Boott. | |
| <i>Salix maccalliana</i> Rowlee. | | <i>Carex utriculata</i> Boott. | |
| <i>Salix candida</i> Fluegge. | | <i>Betula glandulosa</i> Michx. | |
| <i>Salix balsamifera</i> Barr. | | <i>Ribes</i> spp. | |
| <i>Salix mackenziana</i> macrogemma Ball | | <i>Rubus arcticus</i> L. | |
| <i>Calamagrostis canadensis</i> (Michx.) Beauv. | | <i>Rubus strigosus</i> Michx. | |
| <i>Calamagrostis americana</i> Scribn. | | <i>Lonicera involucrata</i> (Richards) Banks | |
| <i>Poa palustris</i> L. | | <i>Epilobium angustifolium</i> L. | |
| <i>Bromus ciliatus</i> L. | | | |

(3) *Gramineta*. Many of these *Gramineta* are very similar to those adjoining sloughs and lakes (*vide* p. 45), the dominant species being *Calamagrostis americana*, *Poa palustris* and *P. pratensis*, whilst others are dominated by *Calamagrostis canadensis*. Accompanying plants include the following:

| | | | |
|--|--|--|--|
| <i>Agrostis hiemalis</i> (Walt.) B.S.P. | | <i>Caltha palustris</i> L. | |
| <i>Glyceria pulchella</i> Nash | | <i>Potentilla palustris</i> (L.) Scop. | |
| <i>Hordeum jubatum</i> L. | | <i>Rumex mexicanus</i> Meisn. | |
| <i>Agropyron Richardsonii</i> (Trin.) Schrad. | | <i>Epilobium densum</i> Raf. | |
| var. <i>tenerum</i> (Vas.) | | <i>Cicuta maculata</i> L. | |
| <i>Bromus ciliatus</i> L. | | <i>Sium cicutaefolium</i> Schrank. | |
| <i>Bromus ciliatus</i> var. <i>denudatus</i> (Wieg.) Fern. | | <i>Ranunculus cymbalaria</i> L. | |
| <i>Carex prairea</i> Dewey | | <i>Erigeron philadelphicus</i> L. | |
| <i>Carex disperma</i> Dewey | | <i>Aster junceus</i> Ait. | |
| <i>Scutellaria galericulata</i> L. | | <i>Aster puniceus</i> L. | |
| <i>Parnassia palustris</i> L. | | <i>Senecio flavovirens</i> Rydb. var. | |
| <i>Stellaria longifolia</i> Muhl. | | thomsoniensis Greenm. | |
| <i>Stachys scopulorum</i> Greene. | | <i>Arnica chamissonis</i> Less. | |

II. *Retrogressive Changes in Muskegs due to Burning.*

(a) *General account of retrogression and subsequent successions.* The mature bog forest as it exists in the Cordilleran area is of rare occurrence in the Parkland. In the latter more extensively cultivated area the destruction of the forests is due to clearing, drainage and especially to burning. So extensive is this destruction that the majority of the muskegs in the Parkland are in the *Ledum*-moor stage.

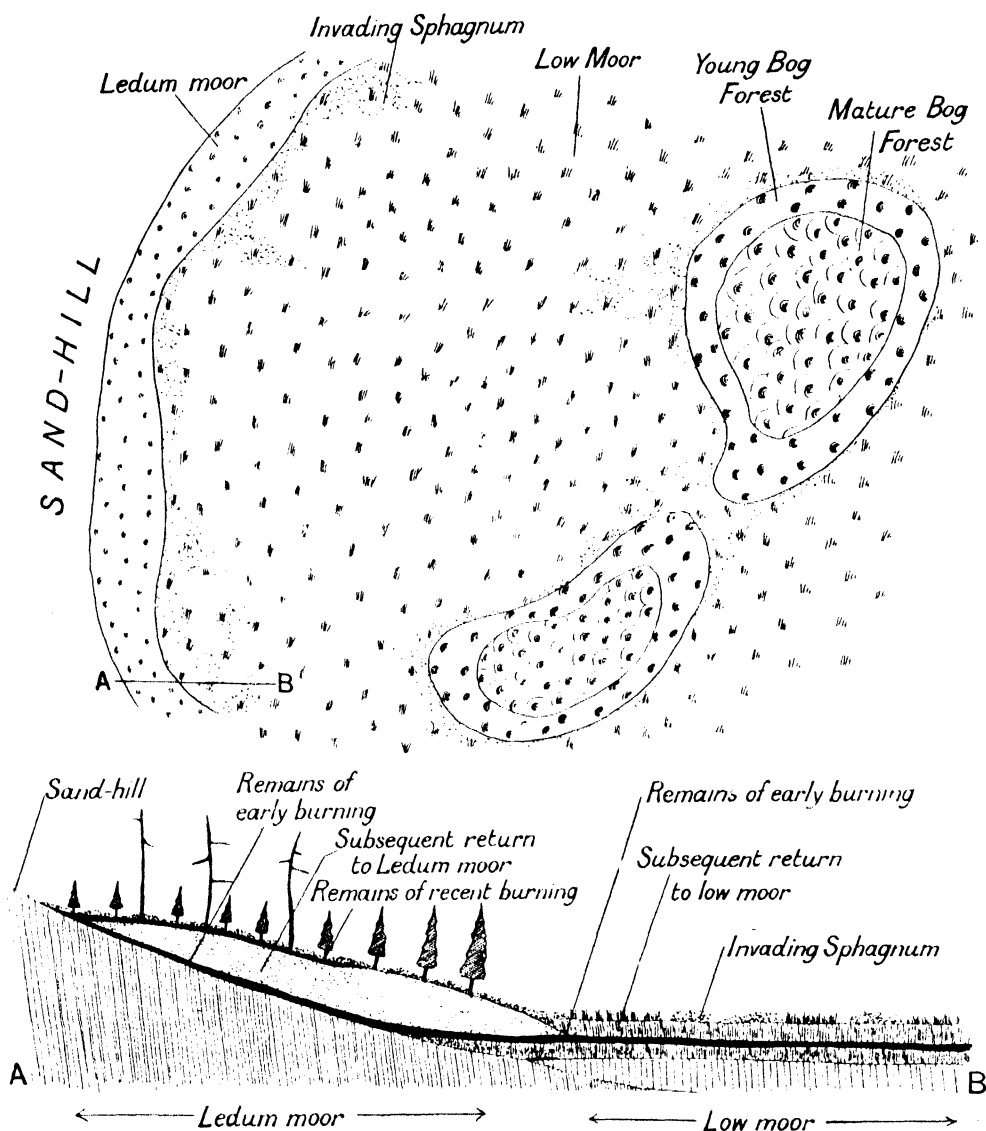
There are, however, one or two remnants of an old bog forest which provide sufficient evidence that the climax of the bog series is similar to that in the Cordilleran area. Before discussing retrogression a description will be given of two relics of the bog forest; the first a young bog forest and the second a mature bog forest.

The young bog forest occurs about 6 miles (9.5 km.) west of Edmonton, and adjoins low-moor. It consists of black spruce about 30 ft. (9 m.) high, the trees being spaced about 6 ft. (1.8 m.) apart with pools of water in depressions at the foot of the trees. The forest floor is covered by mounds of *Sphagnum* about 2 ft. (60 cm.) high, and a luxuriant growth of *Ledum* and other ericaceous plants.

An interesting example of a mature bog forest exists 38 miles (60 km.) west of Edmonton as a series of small areas in low-moor (Area XI). The undergrowth consists of *Hypnum schreberi* Willd., *H. crista-castrensis* L. and *Hylocomium splendens* (L.) Schimp. and broad-leaved mesophytes such as *Caltha palustris*.

Destroyed or partially destroyed muskegs are usually covered not by one but by many associations. This complexity is due to the varying intensity of burning in different parts and is well illustrated in the area surrounding this mature bog forest. The destruction of the trees has been complete in some places whilst in others the trees have been thinned out by the fire. The latter has occurred along the outer fringe of the islands of bog forest, Fig. 5, where, although less than half of the trees have been injured, the growth of *Hypnum* has been replaced by *Sphagnum* and ericaceous plants. Where the destruction of trees has been complete and the peat burned to a considerable depth, sedges and grasses have taken possession. The effect of extensive and deep burning of peat would be to release a large amount of mineral salts and this would at once favour the development of low-moor. This change in the mineral content of the water over a burnt area in comparison with that from the unburnt area is shown in the analyses given below.

The low-moor vegetation which is now generally distributed over this area is becoming invaded by plants of the bog series in the drier localities, i.e. along the margin of the bog, or on the fallen trees in the centre of the bog. Here *Sphagnum* and other *Ledum* moor pioneers are appearing. The return of the *Ledum* moor along the margin as shown in a section, is illustrated in Fig. 5.

FIG. 5. Effects of partial burning on high-moor (*Ledum* moor). Area XI.

| | | | | Parts per million | |
|------------------------|-----|-----|-----|-------------------|---------------------------|
| | | | | Pools in low-moor | Pools in young bog forest |
| Calcium | ... | ... | ... | 33.2 | 18.2 |
| Magnesium | ... | ... | ... | 2.0 | 2.0 |
| Sodium | ... | ... | ... | 1.2 | 1.2 |
| Sulphates | ... | ... | ... | 10.0 | nil |
| Carbonates | ... | ... | ... | 34.7 | 23.6 |
| Silica | ... | ... | ... | 3.2 | 3.1 |
| Iron oxide and alumina | ... | ... | ... | nil | nil |
| Vegetable matter | ... | ... | ... | 73.0 | 120.0 |
| Total solids | ... | ... | ... | 173.0 | 180.0 |

The cause of the persistence of *Ledum* moor round the margin of the low-moor, although burnt at the same period, appears to be due to the following factors. The burning and destruction of the *Sphagnum* covering releases free water if water conservation remains constant in a basin. This results in the flooding of such an area, and an enrichment of the water with mineral salts favouring the development of a low-moor. The boundary of the muskeg frequently rises slightly up the bank. This is a better drained position and free water does not lie here. Thus, if the marginal band has been burnt,—as it has here—it comes back to muskeg at once. In other words, the deep burning of peat may result in the *Ledum* moor being carried back to low-moor. The burning at the margin—even if nearly all the peat is destroyed—is not so effective, as the margin is better drained, and on this the *Sphagnum* starts at once if the precipitation and run-off from the rich humus soil of the bank above is sufficient.

The very common reversion of young bog forests to *Ledum* moor is brought about in the same manner. As the undergrowth is almost identical on both these associations, a fire which kills the trees but leaves the forest floor untouched, results immediately in *Ledum* moor formation, because in a young bog forest, while the *Sphagnum* is usually saturated, the trees of the forest are dry. The activity of rabbits in the Parkland may then hold the vegetation in the *Ledum* moor stage for an indefinite period as described on p. 65.

A more severe burning in a drier season may so change the undergrowth that the return of *Ledum* moor is postponed for a number of years. South-east of Edmonton there are young bog forests that were severely burned about two years ago, which show the early condition of the forest before there is any indication of return to *Ledum* moor. One of these will be described as Area No. XII.

Area No. XII. The severe fire which swept through this forest has left a scene of complete desolation. Every tree, although still standing, is scorched from root to tip, and the peat is badly charred and channelled irregularly by fire. Ridges of peat which still remain, are covered by the charred stems of *Ledum*.

This untenanted ground is already being invaded by pioneers. The first plant to succeed after the fire is *Ledum*, which quickly sends up new shoots from the roots that have escaped burning. The following xerophytic mosses are also found in patches on the burnt peat:

Ceratodon purpureus (L.) Brid.
Webera nutans Hedw.
Leptobryum pyriforme L.

Polytrichum strictum Banks
Polytrichum juniperinum Willd.

In such areas as these the return of *Ledum* moor will probably be a slow process as vegetation must gain a considerable hold before conditions are sufficiently mesophytic for the growth of *Sphagnum*.

In other places, the combined effects of burning, clearing, draining and pasturing of muskegs, have had still more drastic effects, giving a direct suc-

cession to Poplar thicket. An old peat bog three miles (4.8 km.) west of Edmonton will serve as an example. After being cleared and drained, the peat mantle of this bog was almost destroyed by fires which have been known to smoulder for several months under the snow. The peat has been almost entirely burnt off, exposing the underlying clay. No muskeg plants are to be found on the ridges of peat that do remain, their place being taken by small xerophytic mosses. The clay substratum is occupied by a few straggling poplar seedlings and a carpet of closely cropped grass, so that the burnt bog has been practically converted to Parkland.

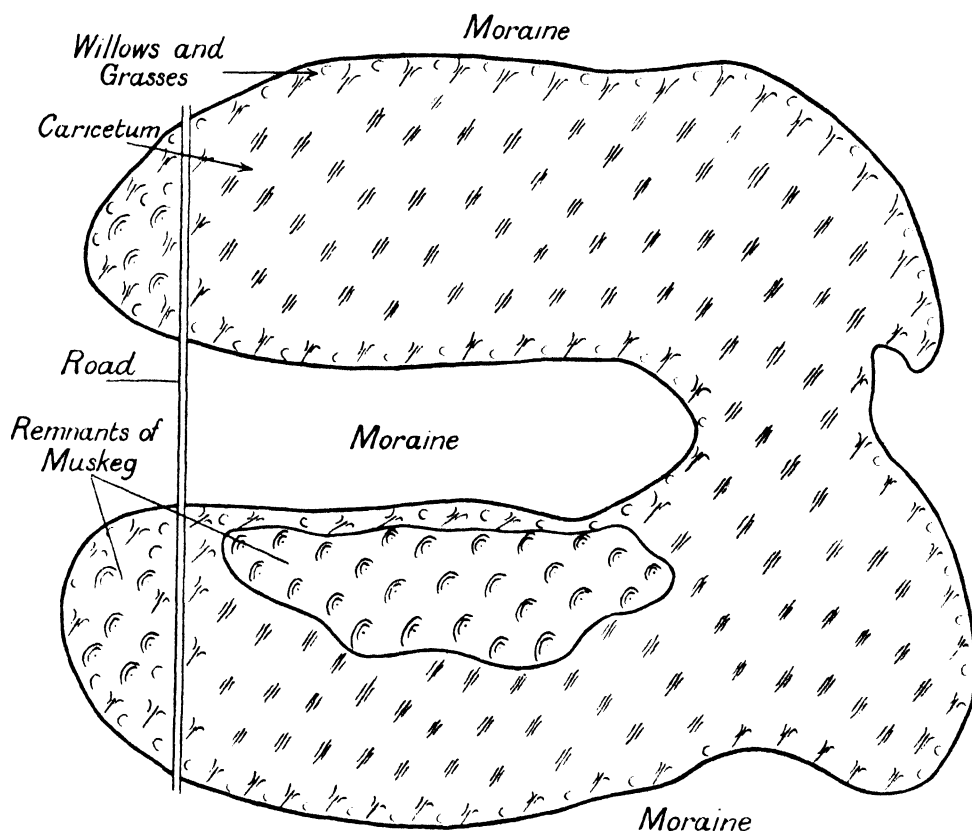


FIG. 6. Showing retrogression of muskeg to low-moor due to burning. Area XIII.

(b) *Vegetation of low-moors formed by retrogressive changes.* Low-moors that have developed from muskeg as a consequence of burning vary floristically according to the extent and frequency of burning and according to the amount of water retained during the growing season. The vegetation of a deeply burned and very wet moor is described below (Area No. XIII), after which composite lists are given of low-moor species that characterise muskegs in various stages of retrogression. It will be noted that the vegetation of denuded muskegs closely resembles that of *Cariceta* and *Saliceta* already described, pp. 56-57.

Area No. XIII. This area occurs in the morainic region of Cooking Lake. It is irregular in shape, consisting of two main parts, each about 400 ft. (120 m.) in length, Fig. 6. Associated with the low-moor are three small patches of dry muskeg, the largest of which is shown in the central part of Plate X, Phot. 20. The muskeg was at one time covered with a fairly close stand of black spruce, as is evidenced by numerous stumps among the trees still standing. The general level of the muskeg is about 10 inches (25 cm.) above that of the adjoining low-moor.

According to an inhabitant of the district, the depression under consideration was completely covered with muskeg less than 15 years ago, and has been regularly burned during dry seasons of recent years. The general appearance of the area at present leads one to suppose that this statement is essentially correct. As a result of burning, all the *Sphagnum* peat has been destroyed on that part of the area now occupied by low-moor vegetation. The latter rests upon a bed of *Carex-Hypnum* peat about four feet (120 cm.) in thickness.

The floor of the low-moor is covered with a thin carpet of *Hypnum* which, in dry seasons, makes very poor growth. On the border of the moor, there is a narrow band dominated by willows and by *Calamagrostis canadensis*, with which are associated *Calamagrostis americana*, *Agrostis hiemalis* and *Bromus ciliatus*. The central and larger part of the moor presents the general appearance of a Caricetum, and is composed of the following species:

| | | | |
|---|-------------|---|------|
| <i>Carex diandra</i> Schrank. | d. | <i>Cicuta bulbifera</i> L. | f. |
| <i>Equisetum fluviatile</i> L. | a. and l.d. | <i>Potentilla</i> sp. | f. |
| <i>Calamagrostis canadensis</i> (Michx.) Beauv. | l.d. | <i>Aster puniceus</i> L. | f. |
| <i>Rubus arcticus</i> L. | l.d. | <i>Senecio eremophilus</i> Richards | f. |
| <i>Menyanthes trifoliata</i> L. | a. | <i>Senecio discoides</i> (Hook.) Britt. | l.a. |
| <i>Potentilla palustris</i> (L.) Scop. | a. | <i>Erigeron philadelphicus</i> L. | s. |
| <i>Salix</i> sp. (small plants) | a. | <i>Geum macrophyllum</i> Willd. | s. |
| <i>Eriophorum chamissonis</i> C. A. Mey. | f. | <i>Habenaria</i> sp. | s. |
| <i>Stellaria longifolia</i> Muhl. | f. | <i>Triglochin maritima</i> L. | s. |
| <i>Scutellaria galericulata</i> L. | f. | <i>Rubus strigosus</i> Michx. | o. |
| <i>Epilobium densum</i> Raf. | f. | | |

The following composite lists will serve to give a general idea of the vegetation of typical wetter and drier portions of denuded muskegs.

Wetter areas

Carex aquatilis Wahl.
C. praegracilis Boott.
C. diandra Schrank.
C. utriculata Boott.
C. canescens L.
C. capillaris L.
Eriophorum chamissonis C. A. Mey.
Equisetum fluviatile L.
Glyceria nervata (Willd.) Trin.
Potentilla palustris (L.) Scop.
Caltha palustris L.
Petasites sagittata (Pursh.) Gray
Scutellaria galericulata L.
Triglochin maritima L.
T. palustris L.
Stellaria longifolia Muhl.
S. crassifolia Ehrh.
S. subvestita Greene
Hypnum spp.

Drier areas

Calamagrostis canadensis (Michx.) Beauv.
C. americana Scribn.
Poa palustris L.
P. crocata Michx.
Agrostis hiemalis (Walt.) B.S.P.
Bromus ciliatus L.
Carex prairea Dewey
C. gynocrates Wormskj. } on *Sphagnum* mounds
C. paupercula Michx. }
Salix planifolia Ph.
S. petiolaris J. E. Smith
S. candida Fluegge
S. bebbiana Sargent
S. serissima (Bail.) Fern.
S. maccalliana Rowlee
S. balsamifera Barr.
Betula glandulosa Michx.
Lonicera involucrata (Richards) Banks
Rubus arcticus L.



Phot. 19. A wet basin with a central quaking mat of *Hypnum-Menyanthes* and Carices. Area No. X (p. 55).



Phot. 20. Low-moor initiated by the burning of muskeg. A large patch of unburnt muskeg is also shown (p. 62).



Phot. 21. Parkland vegetation following the burning and drainage of a large bog.

THE DESTRUCTION OF HIGH-MOOR BY THE INFLUX OF CALCAREOUS WATER.

An example of the destructive effect on muskegs of water highly charged with mineral salts was described in a former paper (1). We have now found four cases of this type all west of Edmonton, and in view of the interest attached to the process and the potential value of the resulting mineral deposits, brief reference may be made to one of these areas.

The best example occurs 6 miles (9.6 km.) west of Edmonton at Winterburn and consists of an extensive stretch of muskeg some miles across. Much of the muskeg bears indication of burning and is now in the condition of *Ledum* moor.

Through the middle of the muskeg runs a strip of low-moor which contains a chain of small lakes. The pools and lakelets of this central area show a few centimetres of clear water and below this a spongy deposit, about 4 feet (120 cm. in thickness), of calcareous material deposited by the algae, mosses and small crustaceans in the water. Partial drainage at the southern end has resulted in the emptying of some of the lakes, leaving the floor consolidated as an expanse of almost pure calcium carbonate.

The features in this area are strikingly similar to those described from the Stony Plain muskeg in a former paper (1). The parallel is further emphasised by the analysis of the calcareous deposit taken from the two areas.

Analysis of Calcareous Deposits.

| | Stony Plain muskeg | Winterburn muskeg |
|----------------------------|--------------------|-------------------|
| Calcium carbonate ... | 64.21 | 80.32 |
| Magnesium carbonate ... | 0.11 | 0.40 |
| Silica ... | 4.51 | 0.29 |
| Iron oxide and alumina ... | 0.43 | 0.04 |
| Vegetable matter ... | 30.65 | 18.91 |

Deposits consisting of practically pure calcium carbonate, of a fine texture requiring no pulverising, is exceedingly valuable material for the treatment of some types of soils not infrequent in this region, and the thickness of the deposit amounting to 4½ ft. (1.3 m.) and its extent, renders such areas of great potential value.

The proximity of these lakes so rich in mineral salts, with a muskeg vegetation is an anomaly which can be emphasised by a table showing the analysis of water from these calcareous lakes, and water taken from an undisturbed part of the young bog forest.

| | | | Parts per million | |
|----------------------------|-----|-----|-------------------|--------------------|
| | | | Calcareous lake | Pool in bog forest |
| Calcium ... | ... | ... | 80.9 | 18.2 |
| Magnesium ... | ... | ... | 34.6 | 2.0 |
| Sodium ... | ... | ... | 1.2 | 1.2 |
| Sulphates ... | ... | ... | 57.7 | nil |
| Carbonates ... | ... | ... | 119.4 | 23.6 |
| Silica ... | ... | ... | 3.0 | 3.1 |
| Iron oxide and alumina ... | ... | ... | nil | nil |
| Vegetable matter ... | ... | ... | 30.0 | 120.0 |
| Total solids ... | ... | ... | 388.0 | 180.0 |

The presence of this alkaline water has resulted, just as it did in the Stony Plain muskeg, in the conversion of high-moor into low-moor, and here also, islands of muskeg still stand in the lake and low-moor as evidence of the former condition of the vegetation.

A description may now be given of this resulting low-moor from the east margin of one of the lakes.

This lake has been drained by a ditch at the south end so that the basin has a greater width than is now occupied by water. As the lake was a little deeper on the west than on the east side, the lowering of the water level

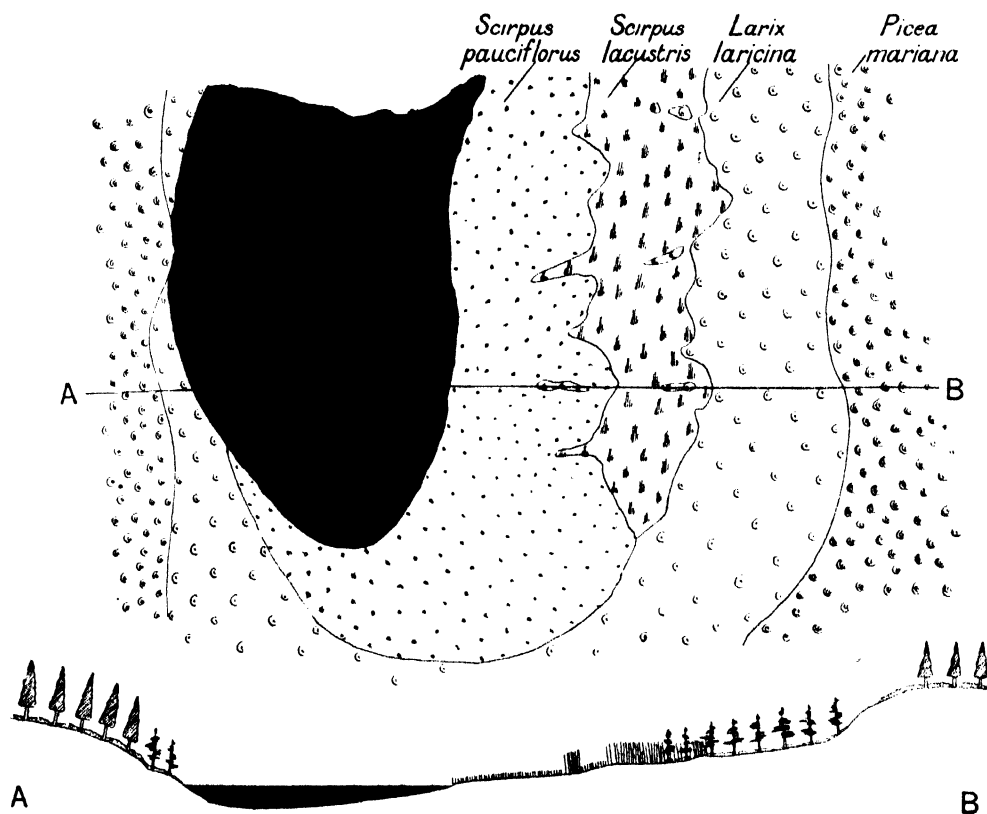


FIG. 7. Topography and vegetation of calcareous area on muskeg near Winterburn.

exposed a flat stretch of ground on the east margin alone, while on the west side the water extends nearly to the old banks. These banks, about 2 feet (60 cm.) high, are of peat and are clothed by muskeg vegetation.

On the level land to the west, the lake is surrounded by four distinct zones, as is shown in Fig. 7.

First, in the shallowest water of the lake and also along its immediate margin is an almost pure stand of *Scirpus pauciflorus* Lightf. together with clumps of *Juncus richardsonianus* Schult.

Outside this is a band of *Scirpus validus* Vahl. which is obviously invading



Phot. 22. Dominance of *Lachum* after severe burning of a bog forest.



Phot. 23. Calcareous area on muskeg (p. 65).

the more hydrophytic association by sending out rhizomes which spread into the area of the smaller *Scirpus*. This is shown in Pl. XI, Phot. 23.

The next association attains its best development at the foot of the peat banks. *Larix laricina* is the dominant tree, with an undergrowth of the mosses:

Hypnum aduncum Hedev. var. *Kneiffi* Schimp.
Camptothecium nitens Schimp.

Leptobryum pyriforme L.

and the following associated plants:

Poa palustris L.
Salix sp.
Betula glandulosa Michx.
Muehlenbergia racemosa (Michx.) B.S.P.

Parnassia palustris L.
Pinguicula vulgaris L.
Habenaria hyperborea (L.) R.Br.

That this will in time invade the more central associations is shown by the presence of outposts of this vegetation on the drier positions afforded by the ridges and fallen logs on the *Scirpus* zone. There we find seedling larch and young willows, while still farther out in the marginal zone of *S. pauciflorus*, the tufts of *Juncus* afford foothold for small plantations about 6 inches across of *Camptothecium*, *Leptobryum* and *Salix*.

Outside the *Larix* zone we come to a rise of ground formed by *Sphagnum* peat, which marks the transition to the *Ledum* moor. The banks of peat abutting on the larch zone show no outposts of invading vegetation which are so well marked with the other three zones. In fact the banks are altogether devoid of vegetation except for such plants as *Polytrichum* and *Vaccinium vitis-idaea* which seem to be particularly tolerant of calcium. The *Sphagnum* of these slopes is dead, the peat brown and decomposed, and it is only on the top of the mounds that we find the *Ledum* moor in anything like its natural condition. There we find living *Sphagnum*, *Ledum*, and an abundance of young black spruce, but in no instance does this vegetation invade the lake margin.

LEDUM MOOR SUB-CLIMAX DUE TO BIOTIC FACTORS.

In this country, which has been recently, and in some districts is now, heavily stocked with game, we might expect biological factors to have produced considerable modification in the natural vegetation. This is more especially the case in regard to the moor series in which the vegetation types are extremely sensitive to the influence of grazing, trampling, and manuring. The animals most probably influencing succession are rabbits, beaver, and, to a much lesser extent, larger game.

During the last 15 years beaver has nearly disappeared from the areas described in this paper, but before this date they must have brought many changes to vegetation lying in basins and valleys. Wood cut by beaver can be found buried in some places in the peat, and old beaver dams are quite frequent. In the general effort to drain bogs and lakes, such dams have been broken by man and no longer function, at any rate in the districts recorded in this paper.

Rabbits are at the present day undoubtedly the biological agents chiefly responsible for changes in types of succession. There is no reason to suppose that rabbits are more abundant now than in former times, but there are decided rhythmical fluctuations in their number; a maximum occurring every 8·5 years, according to a mean of the records between 1845 and 1905. This is not a sharp maximum but is usually regional in character, and the period of abundance covers several years (6). During these maximum periods extensive barking and girdling of poplar and willow occurs and young coniferous trees have the leaders and other young shoots eaten off at snow level. In many muskegs nearly every young tree may be eaten off a few inches above the snow-level of the winter, giving a curious appearance to the muskeg when the snow has melted. While such injury is quickly repaired by deciduous shrubs and young trees, more permanent damage may be suffered by conifers to the extent of death if the main stem is ringed. The great influence of rabbits in the development of heaths in eastern England has been described by Farrow (7), and it is probable that the influence is even more important here owing to the long winter and scarcity of food.

While no precise evidence is available regarding the relative abundance of rabbits in districts characterised by different vegetation formations and associations, there appears to be no doubt that rabbits are far more abundant in the Parkland area than in the coniferous forests of the North and West. This is probably the most important factor in the Parkland tending to prevent the development of climax forest and holding the moor succession at the sub-climax of *Ledum* moor. It has not been possible as yet to carry out any experiment with rabbit-proof netting, but we have frequently observed that when one of the little muskegs which are so frequent westward of Edmonton lies near a village the muskeg is generally more closely tree clad. This is well seen just outside the village of Entwistle where a small muskeg is covered with seedlings of *Picea mariana* of a uniform height of about 2 ft. (30 cm.) almost as thickly as they can stand. *Sphagnum* here has almost disappeared and even *Ledum* is becoming killed off by the dense shade of the small trees. While this may be regarded as only a very young stage of a bog forest, the existence of such features in places where rabbits tend to be excluded suggests that the *Ledum* moor of the Parkland is a sub-climax of a permanent nature produced partly, at any rate, by rabbits and partly by fire.

THE DEPOSITS UNDERLYING THE MOOR SERIES.

In nearly all the areas described in this paper the deposits underlying the peat have been reached either by boring or by sections, and analyses of the clays have shown a remarkable uniformity in physical and chemical characteristics. In some cases fossil remains, either on the surface or embedded at some depth below the surface of the clay, have been discovered, and while these are not numerous as regards genera or species they do throw some light

on the conditions before the peat began to be formed, and suggest several interesting problems for future investigation.

The character of the under clays in the Edmonton district was described in a former paper (1) and it is remarkable that over so great a stretch of country there should be so little variation. Samples of four clays underlying various moors described in this paper have been analysed and are given below, and the other very numerous samples from beneath other bogs which have been examined in the field agree in appearance and general characters.

| | Area XI (p. 58) | Boag Lake muskeg, Cooking Lake Area | McLeod bog (p. 32) | Low-moor Area VII (p. 53) |
|-----------------------|--------------------|--|--------------------------|---------------------------------|
| Silica | 55.40 | 78.30 | 66.80 | 79.38 |
| Iron oxide | 2.42 | 4.12 | 1.50 | 0.10 |
| Alumina | 9.18 | 9.68 | 18.24 | 11.82 |
| Lime | 14.18 | 0.31 | 4.72 | 1.37 |
| Magnesia | 0.20 | 0.28 | 0.89 | trace |
| Alkalis | 2.40 | 2.16 | 1.67 | 0.31 |
| Manganese | trace | trace | — | — |
| Organic matter | 16.22 | 5.15 | 6.18 | 7.02 |

The fossil plants from the surface layers of these clays may be briefly described on a regional basis because of the somewhat different history and stages of the peat lying upon them.

I. Further samples of the clay below Stony Plain muskeg have been examined and the following additions have been made to the list published in 1926 (1):

- | | |
|---|--|
| 1. Hypnum scorpioides L. | 7. Amblystegium radicale (P.B.) |
| 2. H. stellatum Schreb. | 8. Camptothecium nitens Schimp. |
| 3. H. fluitans L. | 9. Amblystegium filicinum (L.) De Not. |
| 4. Sphagnum acutifolium Ehrh. | 10. A. serpens (L.) B. and S. |
| 5. Sphagnum sp.—may be a different species or variety | 11. Sphagnum sp. Sect. acutifolia |
| 6. Bryum sp. probably B. pallens Ew. | 12. Zannichellia palustris. |

II. *Sphagnum island bog*—from the surface of the clay underlying *Sphagnum* area:

- | | |
|--------------------------------|---|
| 1. Hypnum sendtneri Schimp. d. | 3. Sphagnum sp. Sect. cuspidata |
| 2. H. cuspidatum L. | 4. Fragments of other harpidioid Hypna. |

III. *Sphagnum island bog. Clay underlying Carex zone:*

- | | |
|--------------------------------|-------------------------|
| 1. Hypnum sendtneri Schimp. d. | 2. Hypnum cuspidatum L. |
|--------------------------------|-------------------------|

Fourteen miles east of Edmonton lies a fairly extensive bog of the *Ledum* moor stage similar to others described elsewhere. Sections have been cut through the peat 4 ft. (1.2 m.) deep to the underlying clay. The work was carried out towards the end of a fairly dry season and an attempt was made to reach the bottom of the clay. Much difficulty was experienced owing to the tenacity of the clay, which had to be scraped off the spade with an axe, for each cut, and to the amount of water seeping in. Further work was stopped by snowstorms and rain, but a depth of about 3½ ft. (1 m.) in the clay was reached.

At 22 inches (56 cm.) below the surface of the clay underlying this muskeg, wisps and lenticular patches of humus were found embedded in the clay which elsewhere was nearly free from organic matter. This material was carefully collected and worked through in the laboratory, and yielded *Sphagnum magellanicum* Brid., *Sphagnum* sp., *Sphagnum acutifolium*, *Sphagnum* sp.—a portion of a branch of a submerged species of the acutifolia group. Amongst the clay at the same level was the remains of a fungus which could be dissected out from the clay. A considerable amount of this was obtained and some mounted in Canada balsam slides and sent to Dr E. J. Butler, of the Imperial Bureau of Mycology, who reports that “This fungus comes very close to the fungal partner known as *Endogone* in the common type of endotrophic mycorrhiza found in many parts of the world. It also bears a close resemblance to certain fossil genera such as *Palaeomyces*.”

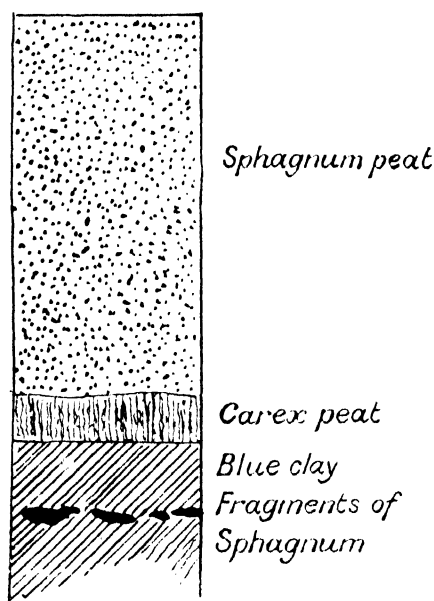


FIG. 8. *Sphagnum* embedded 22" below surface of blue clay. Near Boag Lake 14 m. E. of Edmonton.

The character of this material embedded in the clay at some depth below the surface is surprising, and suggests that the deposition of the clay and the beginning of peat growth represent a long series of changes. The relationship of the beds in this section is illustrated in Fig. 8. It is difficult to explain the presence of isolated leaves and small branches of *Sphagnum* and of the remains of fungi so far down in the clay. As pointed out elsewhere in this paper, the recession of the ice was probably very unequal, and muskegs may possibly have existed in other situations than in the basin now described. In that case there would be the possibility that this represents drifted material from contemporary muskegs, but a solution to the question must await further work.

In conclusion, we should like to express our cordial thanks to Dr M. O.

Malte, National Herbarium, Ottawa, for critical determination of the grasses and sedges and some other plants; to Mr H. N. Dixon, who very kindly examined many of the recent and all the sub-fossil mosses; to Dr C. R. Ball, who made a critical examination of the willows; to Dr J. M. Greenman, Curator of the Missouri Botanical Garden, for determinations of *Senecio*; and to Dr E. J. Butler, Director of the Imperial Bureau of Mycology, who examined the fungus remains found in glacial clay.

SUMMARY.

The types of swamp, moor and bog forest vegetation in three of the phytogeographical regions of Central Alberta have been described. The areas lie in morainic basins of varying size, and the blue glacial clay under the peat deposits contains numerous mosses and the seeds of water plants inhabiting the lakes before the formation of the low-moors and high-moors which now occupy these basins.

The *pH* of the low-moors varies from 5.0 to 6.5 and the high-moors 4.0 to 5.5. Analyses of the clays and the free water in types of swamps, low-moors and high-moors are given.

The vegetation is described from a regional point of view under the three climatic climax formations characteristic of Central and Northern Alberta, viz., the Cordilleran Forest, Northern Forest, and Poplar Parkland. In the Cordilleran Forest area the three most widely distributed formations banding lake margins are low-moors (*Cariceta*), birch bogs and bog forest. Centrifugal growth of *Sphagnum-Andromeda* (the earliest association of the *Sphagnum* succession) is rare, and has been met with in only one basin. Birch bogs are developed as primary associations in large deep basins where much of the ground is covered with *Hypnum revolvens* with a flora in which Ericaceae are absent. Larch is associated with the birch, the latter usually being confined to the ridges formed by the long horizontal roots of the larch. The floras of the ridges and the flat depressions between are strongly contrasted. Mature bog forest formed of old black spruce with a floor of *Hypnum crista-castrensis* L. and *Hylocomium splendens* and a scanty non-ericaceous flora forms the climax of the bog succession. The general succession in the Northern Forest resembles in broad features that of the Cordilleran Forest. Marginal muskegs encroaching on central low-moor (*Cariceta*) are frequent and are present as primary successions in some basins, *Sphagnum* spreading centripetally into the *Caricetum*. Marginal muskegs are also present as a secondary succession, and in such cases mounds of the original high-moor are often found scattered over the secondary low-moor; their survival being due to irregular burning. Small muskegs in which the original *Sphagnum*-ericaceous vegetation has entirely disappeared occur near the southern boundary of the Northern Forest. White spruce and poplar have occupied these areas.

In the Parkland reed-swamp and low-moors are usually associated with

sloughs and lakes. Swamps are formed of various associations of rushes, sedges and grasses, while low-moors may be dominated by *Cariceta*, *Saliceta* or *Gramineta*. The high-moors are generally at the *Ledum* moor stage and examples of climax bog forest are rare. The succession of associations within the various formations are described, and the effects of burning, drainage, mowing, grazing and other factors are discussed.

The destruction of high-moors by the influx of springs rich in calcium salts is described, and the activity of algae acting under such conditions has resulted in extensive mineral deposits ranging as high as 80 per cent. calcium carbonate.

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COCKSFOOT GRASS (*DACTYLIS GLOMERATA* L.): ECOTYPES IN RELATION TO THE BIOTIC FACTOR

By R. G. STAPLEDON, M.A.

(With Plates XII—XVII, containing twenty-four Photographs.)

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INTRODUCTION.

In the case of most of those grasses which are mainly sward-forming species, or which, at all events, tend to grow in relatively closed associations, differences as between plant and plant within the species are often not strikingly manifest when individuals are examined in their natural or semi-natural habitats. This is, of course, largely true of innumerable species which grow in close association with other species or in gregarious masses. But Turesson (11), for example, has shown that, by making collections of representatives of a particular species from devious and characteristic habitats and growing the plants thus collected as spaced individuals under one and the same set of uniform garden conditions, very striking differences in growth-form and frequently also in more intimate morphological characteristics as between the representatives of various habitats are revealed.

As a result of very complete investigations conducted on these lines with a number of species, Turesson has recognised within the Linnean species the existence of what he has justly termed "ecotypes"; being "the products arising as a result of the genotypical response of an ecospecies to a particular habitat." It would follow from the work of Turesson that the representatives of any particular species found growing on any particular habitat would be most unlikely to represent either phenotypically or genotypically the whole potentialities of that Linnean species. It would seem probable, moreover, that the more characteristic—the more pronounced—the edaphic, biotic and climatic controlling factors of a particular habitat, by that much the greater would be the limitation of the phenotypes and genotypes of even the successful species contributing to that habitat. The limiting and selective effect of environmental factors on the ultimate types within a particular species is abundantly proved by an intensive study of any of the herbage species indigenous to Europe which have also been introduced and extensively grown (and seed crops taken year after year) in North and South America, in Australia and New Zealand. The recent critical studies of Williams (12) on red clover, apart altogether from their agronomic importance, are, for example, of the greatest possible biological significance in relation to Turesson's enunciation of the importance of the concept of ecotypical selection.

An intensive study of any species very soon reveals how manifold are the characteristics in which plants of the same species can vary, and at the same time shows how wonderfully true to these subtle differences particular plants remain year after year. In the present state of our knowledge we write and think in terms of phenotypes—types which we can readily recognise and describe; it is highly probable, however, that within the phenotype there exist perhaps many, perhaps few, "response-to-differential-habitat" types which at present we are unable to recognise; but which, if in fact they exist,

would be as important in relation to ecotypical selection acting upon the genotype as are the phenotypes themselves.

That our ordinary tests for the recognition of variety, strain, type or form, call the distinction what we will, are very far from adequate—adequate in the sense of correlating physiological-morphological-genetical adjustment with the dictates of habitat—is suggested on the one hand by the innumerable yield and other studies now in progress at the Agricultural Stations, and on the other by the recent work of Garner and Allard (4), Tincker (10) and others on the effect of the duration of daylight on the flowering and fruiting of plants.

It would therefore perhaps follow that the biological implication of ecotypical selection as proved to take place in innumerable species by Turesson, in red clover by Williams, and in cocksfoot as implied by Gregor and Sansome (5) and further established in the present paper, has, in fact, a greater significance than can be proved by our present methods of examining and categorising plants.

Turesson has concerned himself for the most part with extreme habitats: sea cliffs, inland, alpine, upland, and with widely separated geographical positions—in short, with the edaphic and climatic factors. In the present study the chief and deciding factor under review has been the biotic, in this case man's control of his grazing animal, a factor which in the present "occupied" state of the world has to be recognised as perhaps the master factor influencing the vegetation of a preponderant proportion of the earth's surface.

MATERIAL AND METHODS.

The writer's attention was first drawn to the extreme variation in the species *Dactylis glomerata* when making a tour of the grasslands of the country in 1918 in connection with the work upon which he was then engaged on behalf of the Food Production Department of the Ministry of Agriculture. During the summer of that year he was able to make a number of collections and to interest others in the matter. The Welsh Plant Breeding Station was founded in 1919 and it was then possible to make arrangements for growing plants from the collections, to add very materially to the scope of the work and to continue collecting material on a more exhaustive basis.

The procedure adopted has been as follows. Plants have been dug up *in toto* from characteristic habitats and seed has been collected; in addition, seed samples have been obtained from all the ordinary commercial sources of origin. In all, 458 collections have been made, comprising 30 seed samples from Denmark; 8 from France; 11 from U.S.A.; 7 from Sweden; 21 from New Zealand; 66 from various habitats in Britain; besides 315 individual plants which have been dug up from representative habitats in England, Scotland and Wales.

The seed has been sown in sterilised soil in boxes in a heated greenhouse during December–January and the seedlings, after being hardened off, planted

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out with wide spacing as weather has permitted in May, June or July. Critical study of the plants has commenced during the season following the planting out. The plants dug up have usually been broken into two or more separate propagants and planted out with wide spacing. These have also been studied in the season following planting.

In all, 11,328 individual plants, the outcome of the 458 collections, have been brought under critical study—on these plants, that is to say, various notes have been taken and in the case of a very large proportion of them a considerable amount of accurate quantitative as well as qualitative data have been obtained.

In addition to a study of the plants directly derived from the collections, representative plants of all the chief types have been selfed and the progeny plants brought under review. In all, 14,935 progeny plants from selfing have been set out as widely spaced plants and have been brought under critical study, in many cases supported by the collection of quantitative data. A number of the selfings have now been carried to the third generation, while the vast majority have been carried to the second generation.

It should be pointed out that this work was undertaken almost entirely with agronomic ends in view, the aim being to select and breed valuable strains of cocksfoot for agricultural purposes. This paper is therefore based on data that were not originally intended to throw light on the problem of ecotypes. So striking were the differences between the various collections that it early became evident that, in the case of a cross fertile plant like cocksfoot, some understanding of the etiology of ecotypical selection must necessarily form the ground-work for subsequent controlled breeding.

It is not possible in this paper to present all the mass of data that have been collected, while as the work has advanced the methods of classification have necessarily been modified from time to time. Consequently the quantitative data have not been obtained on precisely the same lines during each of the eight years that spaced plants have been under study.

The chief evidence under review relates to "growth-form," that is to say, to characteristics of the plants that are admittedly difficult to describe and define. Much therefore depends upon the personal equation of the investigator in assigning plants to their respective groups—intermediate forms naturally presenting great difficulty.

It will perhaps be conceded, however, that an investigator concerned with a single species, and who has had the opportunity of examining several thousand plants for eight consecutive years, may claim to be able to assign individual plants to particular growth-form groups with no mean degree of accuracy and reliability. From the biological point of view it is not the accurate definition and description of the groups that matters—what matters is that the groups should in fact represent a real strain corresponding with a definite phenotypical and genotypical constitution of the plants so grouped. The

reality of the growth-form differences has been readily apparent to those to whom it has been possible to demonstrate the classification adopted by reference to the living plants which have formed the basis of the present studies. An endeavour has been made to illustrate the major differences by resort to photographs. The obtaining of reliable photographs has, however, not been easy. In the first place, photographs of plants *in situ* have not proved satisfactory, and, in the second place, comparative photographs have to be taken contemporaneously and at the correct growth stage, an exceedingly difficult matter in a district with a very unreliable climate. In addition to this, a photograph does not do full justice to a very dense plant compared to one somewhat less dense. And, finally, at a Plant Breeding Station "type" plants are valuable and a limit has to be set to the number of plants that it is possible to dig up at the appropriate stage of growth for the purpose of photographing.

MORPHOLOGICAL CHARACTERISTICS.

Although differences in the character of stem, leaf and inflorescence are not to any striking extent correlated with differences in growth-form as between the different types of cocksfoot, it is perhaps of interest briefly to refer to some of the more obvious of the variations met with in the species.

Vegetative characters. Cocksfoot is invariably described as glabrous: plants occur, however, which show very considerable hairiness on the sheath. The extent of this pubescence shown by hairy plants varies within wide limits. There is no evidence to suggest that this characteristic is in any way connected with habitat relationships.

The margin of the blade of the leaf is serrated, these serrations, however, as has also been shown by Christoph (1), are highly variable as between plant and plant.

There is a wide range of variation in respect of width and length of leaf, one of the more striking of the obvious differences between plant and plant being that between the narrow and broad leaved forms. The width of panicle leaves varies from 0.5 cm. to 1.20 cm., while the length varies from about 13 cm. to 33 cm. The radical leaves of cocksfoot are extremely long when fully grown, ranging from about 21 cm. to 76 cm.

Inflorescence. The panicle characteristics of cocksfoot show wide variation, but all the forms that have come under study fall into one of seven fairly well-defined classes. These classes are as follows:

Class I. Panicles with main rachis erect and with at least the lowest branch of the panicle spreading outward and downward, making an angle of 90° or over with the vertical main rachis¹ (Phot. 1).

Class II. Panicles with main rachis erect and with at least the lowest

¹ By "main rachis" is here meant that part of the rachis from the lowest node of the panicle and its apex.

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branch of the panicle spreading, making an angle of over 30° but less than 90° with the main rachis (Phot. 2).

Class III. Panicles erect. None of the main branches spreading from the vertical main rachis by more than 30° (Phot. 3).

Class IV. Panicles semi-erect—that is to say, with the main rachis inclined from the vertical to some degree, but not by more than 45° . The lowest or all the main branches spreading outwards and downwards, making an angle of 90° or over with the vertical (Phot. 4, on the right).

Class V. Panicles semi-erect. Lowest or all the main branches making an angle of less than 90° with the vertical (Phot. 5, on the left).

Class VI. Panicles drooping, with the tip of the main rachis inclined from the vertical by more than 45° . The main branches spreading and making an angle of 90° or over with the vertical (Phot. 5, on the right).

Class VII. Panicles drooping, with the main branches making an angle of less than 90° with the vertical (Phot. 4, on the left).

The grouping of the panicles on the basis adopted was the outcome of the critical examination of over 350 carefully selected type plants, which had been chosen as truly representative of the panicle characteristics of the species after an examination of nearly 2000 plants collected from innumerable habitats and sources and which may be assumed to have exhibited the complete range of forms proper to the species.

Considering the panicles as of three main classes—erect, semi-erect and drooping—it is of interest to note that approximately 60 per cent. of the plants examined had erect panicles, about 36 per cent. semi-erect and about 10 per cent. drooping.

The vast majority of the panicles of cocksfoot are tinged (i.e. glumes and/or pales light brown to purple), occasional plants are, however, found with this tint lacking when by comparison the inflorescences have a semi-white appearance, being in fact a light green. The number of light paniced plants so met with in the case of the material under review has been approximately one per cent. of the total number of plants examined¹.

GROWTH-FORM.

Cocksfoot is a strongly caespitose grass, more than one generation of shoots being usually formed in each growing season. The leaf shoots do not normally develop into stem and panicle shoots till after the lapse of one or two years. The relation of panicle shoots to barren shoots at any particular time will be affected by conditions of soil fertility in so far as particular plants are concerned: it is, however, in respect of the potentialities of the different plants

¹ The classification of panicles here given is due to **Dr J. G. Davies (2)** who carried out the work in connection with investigations embodied in his thesis (unpublished) on "The Genetics and Cytology of *Dactylis glomerata*," presented for the Ph.D. degree at Aberystwyth.

in regard to tiller development that the most striking differences between growth-forms manifest themselves.

Tiller development and the relation of the different types of tiller to each other are of course regulated by the plant's seasonal periodicity and must therefore be studied in close relation to growth stage. The growth-form of grasses is best studied, or at all events most easily categorised, during the heading stage—when the inflorescences are commencing to be exerted.

It is very important to emphasise that in dealing with growth-form we are concerned with an aggregate of quantitative characters and with potentialities. Thus in the case of two distinct growth-forms "A" and "B," "A" will always differ from "B," but the range of difference will be vastly different according to time of the year, soil and climatic conditions.

A dry season such as 1921 or 1925 is perhaps more advantageous for the study of growth-forms than a wet and good growing season—a dry period before and covering heading stage is particularly favourable for the accurate grouping of plants according to growth-form.

Contrasting characteristics. The classification of cocksfoot into growth-form types has been based on a study of the following major contrasting characteristics.

(1) *Density—Laxity.* Broadly speaking, a dense plant is not only one which produces a large number of tillers but is such that both barren and panicle tillers grow away more or less contemporaneously in the spring—thus at the heading stage a dense plant will show a high proportion of comparatively large and well grown barren tillers. A dense plant will usually flower later than a lax plant and will flower over a longer period. A lax plant, particularly in a dry year, will not develop barren tillers until the panicle tillers have grown well away, and in extreme cases will not do so to any appreciable extent until practically all the panicles are exerted or even subsequent to flowering. The flowering tillers all come away together, are particularly strong and vigorous, and will all come into flower more or less contemporaneously.

(2) *Erect—Inclined.* In some plants, when tiller elongation takes place from the commencement, the upward growth will be practically vertical. In other cases the tillers will grow away at a wide angle, the plant remaining wide spreading even at the flowering stage. There is a considerable range in this respect. The difference is most easily expressed by measuring at the heading stage (1) the vertical height from the ground to the ligule of the upper leaf of an average panicle shoot, and (2) the distance across the plant from the upper ligule of a shoot on one side to the upper ligule of a shoot on the other. In the tables which follow, this characteristic is expressed as the ratio height/diameter.

(3) *Tall—Short.* The height of the plants varies within wide limits. Height has been obtained by measuring to the apex of an average panicle some little time after the commencement of flowering.

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(4) *Rapidity of growth.* This important characteristic has been recorded by measuring the length of tillers up to the ligule of the highest leaf at various dates throughout the growing season. At each measurement the average of the longest tillers is always taken.

(5) *Relative internodal elongation.* The general character of a plant is affected very much by the extent to which the leaves are lifted off the ground and thus by the relative length of the internodes from the base to the apex of the plant. Some plants have the appearance of being "leafed up" to a high and some to a low proportion of their total height.

(6) *Ratio leaf to stem.* This is a ratio much affected by season and soil fertility, but it is one in which there is the widest potentiality for extreme differences as between strain and strain. The stem and leaf analyses have been conducted by separating the blade or lamina of the leaf from the sheath at the ligule. In these analyses, therefore, sheath has been placed with stem--the "leaf" being the blade or lamina only¹.

(7) *Bulk or yield.* From the agronomic point of view yield is all important--yield is, however, a remarkably characteristic feature of a plant and deserves close attention in connection with any system of classification based on growth-form. The yield data presented in this paper have been based on green weights (taken on a dry day) most usually when the plants have been in full flower.

(8) *Earliness or Lateness.* The range of flowering date between different plants of the same species is very great. In connection with growth-form, moreover, practically all herbage plants show a marked contrast between the early and late forms. This is particularly well shown in red clover, is in strong evidence in white clover, and in many of the grass species, notably timothy and cocksfoot.

Flowering date has been critically studied in connection with the investigations under review. It has been usual to note the date of first exertion of inflorescences (arbitrarily taken when three inflorescences have first broken sheath) and the date of zenith of flowering. The former observation can be made with considerable accuracy, while the latter cannot be held to be absolutely correct within the limits of a day or two.

The range of dates given by cocksfoot is shown in the statement hereunder:

1921. The first plant to flower freely was recorded on May 24th, and the last on June 28th.

1924. The first plant to exert its inflorescences was recorded on May 15th, and the last on June 1st. Flowering was first noted on June 11th, the latest plant to flower was recorded for June 29th.

1925. Exsertion of panicles was first noted on April 30th, the latest plant

¹ This procedure has been adopted because in connection with chemical investigations in progress at the Welsh Plant Breeding Station it has been found that sheath is more closely related to stem proper than to blade or lamina.

not exerting its inflorescences until June 6th. The first plant to commence flowering did so on June 3rd, and the last plant to flower was recorded on June 30th.

It will be noted from the above that the figures vary from year to year, but that the range is considerable every year. The data collected show, however, that the relation of different plants to each other in respect of flowering remain remarkably constant, the plants taking very much the same relative positions year after year.

CLASSIFICATION INTO "GROWTH-FORM" GROUPS.

For the purposes of the present paper it is only necessary to give detailed particulars of six of the main vegetative growth-form groups into which it has been possible to classify cocksfoot. These will be referred to respectively as: lax hay, dense hay, cups, tussocks, spreading pasture, and dense pasture. They are illustrated in Photographs 6-24, Plates XIII-XVII.

Table I. *Showing the chief characteristics of four main (vegetative) groups of cocksfoot. 1921.*

| Group | Total wt. (green in oz.) of hay and after- math | Percent. leaf in hay | Total no. of tillers | Percent. barren tillers | Percent. early produced barren tillers | Ht. to apex of panicle in cm. | Percent. number of plants which flowered | | |
|-----------|--|----------------------------|----------------------------|-------------------------------|--|--|---|--------|------|
| | | | | | | | Early | Medium | Late |
| Lax hay | 35 | 21 | 139 | 27 | 15 | 111 | 62 | 36 | 2 |
| Dense hay | 38 | 31 | 192 | 41 | 26 | 98 | 14 | 60 | 26 |
| Tussocks | 39 | 31 | 185 | 38 | 27 | 100 | 17 | 58 | 25 |
| Pasture | 29 | 45 | 203 | 59 | 28 | 80 | 14 | 42 | 44 |

Table II. *Showing the chief characteristics of three main (vegetative) groups of cocksfoot. 1922.*

| Group | Total wt. (green in oz.) of hay, aftermath and pasture | Percent. leaf in hay | Total no. of tillers | Percent. barren tillers | Ht. to apex of panicle in cm. | Height/ Diameter | Length of radical leaves |
|------------|--|----------------------------|----------------------------|-------------------------------|--|---------------------|--------------------------------|
| | | | | | | | |
| Dense hay* | 45.7 | 19 | 196 | 31 | 100 | 0.9 | 46 |
| Tussocks | 39.3 | 16 | 220 | 39 | 92 | 0.8 | 42 |
| Pasture | 28.0 | 28 | 284 | 49 | 84 | 0.7 | 27 |

* Lax hay plants were not included in this trial which consisted only of indigenous collections.

Table III. *Showing the chief characteristics of three main (vegetative) groups of cocksfoot. 1923.*

| Group | Total no. of tillers | Percent. barren tillers | Height to apex of panicle in cm. | Length of panicle leaves | Ht. to ligule 2/5 as a percent. of ht. on 5/6 | Date of heading |
|----------|----------------------------|-------------------------------|---|--------------------------------|--|--------------------|
| | | | | | | |
| Hay* | 203 | 22.6 | 113 | 33.4 | 35.4 | 18/5 |
| Tussocks | 283 | 30.0 | 110 | 32.1 | 30.5 | 24/5 |
| Pasture | 283 | 36.0 | 90 | 20.1 | 25.6 | 3/6 |

* Including lax and dense plants.

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Table IV. *Showing the chief characteristics of six main (vegetative) groups of cocksfoot. 1925.*

| Group | Total wt. (green in oz.) of hay | Per- cent. leaf in hay | Per- cent. sheath in hay | Total no. of tillers | Per- cent. barren tillers | Ht. to apex of panicle in cm. | Height/ Diameter | Length of radical leaves | Date of exer- tion | Date of flower- ing |
|-------------------|---|---------------------------------|-----------------------------------|----------------------------|------------------------------------|--|---------------------|-----------------------------------|-----------------------------|------------------------------|
| Lax hay | 20.7 | 15 | 10 | 179 | 33 | 110 | 1.14 | 55.2 | 14/5 | 13/6 |
| Dense hay | 31.5 | 17 | 19 | 337 | 40 | 108 | 1.07 | 58.5 | 23/5 | 18/6 |
| Tussocks | 33.0 | 15 | 25 | 328 | 35 | 99 | 0.62 | 55.5 | 24/5 | 20/6 |
| Cups | 30.4 | 17 | 15 | 228 | 32 | 103 | 0.43 | 46.0 | 20/5 | 17/6 |
| Spreading pasture | 24.4 | 18 | 20 | 272 | 33 | 83 | 0.41 | 46.8 | 25/5 | 20/6 |
| Dense pasture | 24.8 | 21 | 27 | 396 | 36 | 86 | 0.37 | 41.4 | 22/5 | 22/6 |

Table V. *Showing relation of panicle to barren tillers for six main (vegetative) groups of cocksfoot. 1927.*

| Group | Total number of tillers | Percentage panicle tillers | Percentage barren tillers |
|-------------------|----------------------------|-------------------------------|------------------------------|
| Lax hay | 115 | 60.2 | 39.8 |
| Dense hay | 255 | 49.3 | 50.7 |
| Tussocks* | 553 | 41.6 | 58.4 |
| Cups | 155 | 64.5 | 35.5 |
| Spreading pasture | 375 | 25.2 | 74.8 |
| Dense pasture | 419 | 26.4 | 73.7 |

* Representing extra large tussocks.

Table VI. *Showing heights to ligule during the growing season as a percentage of the final height to ligule at the zenith of flowering for six main (vegetative) groups of cocksfoot. 1927.*

| Group | Heights to ligule as a percentage of final height on | | | | | | | | |
|-------------------|--|-------|-------|-------|-------|-------|-------|-------|------|
| | 17/4 | 27/4 | 8/5 | 16/5 | 22/5 | 26/5 | 2/6 | 10/6 | 17/6 |
| Lax hay | 8.10 | 12.40 | 18.60 | 35.40 | 48.90 | 64.10 | 75.30 | 93.80 | 100 |
| Dense hay | 6.98 | 11.20 | 15.60 | 27.00 | 40.00 | 53.20 | 67.50 | 91.30 | 100 |
| Tussocks | 6.46 | 10.80 | 15.50 | 24.00 | 34.60 | 48.40 | 67.80 | 87.10 | 100 |
| Cups | 8.00 | 11.80 | 17.50 | 30.60 | 40.60 | 56.70 | 70.40 | 88.90 | 100 |
| Spreading pasture | 5.60 | 9.60 | 14.50 | 24.10 | 36.30 | 46.10 | 63.00 | 85.30 | 100 |
| Dense pasture | 4.70 | 7.20 | 13.90 | 22.30 | 32.80 | 41.40 | 57.80 | 85.60 | 100 |

Table VII. *Showing the grouping of the panicles into height classes for plants representative of the six main (vegetative) groups of cocksfoot. The figures represent the percentage number of panicles (per average plant) falling into each height class. 1927.*

| Group | Height classes | | | | |
|-------------------|--|---|---|---|---|
| | 80 to 100 per cent. of max. height | 60 to 80 per cent. of max. height | 40 to 60 per cent. of max. height | 20 to 40 per cent. of max. height | Less than 20 per cent. of max. height |
| Lax hay | 73.1 | 22.2 | 4.4 | 0.3 | 0.0 |
| Dense hay | 57.3 | 37.0 | 5.3 | 0.4 | 0.0 |
| Tussocks | 31.9 | 47.6 | 18.6 | 1.8 | 0.1 |
| Cups | 43.8 | 38.4 | 14.0 | 3.8 | 0.0 |
| Spreading pasture | 22.4 | 44.7 | 22.8 | 9.5 | 0.6 |
| Dense pasture | 18.1 | 41.1 | 28.0 | 11.9 | 0.9 |

Table VIII. *Showing the percentage contribution to the total length of the stem (to the base of the panicle) of each of the internodes for five main (vegetative) groups of cocksfoot. 1922.*

| Group | Internodes from apex to base of stem | | | | | | | | | | |
|---------------|--------------------------------------|------|------|------|------|-----|-----|-----|-----|-----|-----|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| Extra lax hay | 16.7 | 31.0 | 19.6 | 15.4 | 10.2 | 4.2 | 1.5 | 1.0 | 1.0 | — | — |
| Lax hay | 14.6 | 33.2 | 20.6 | 14.1 | 9.2 | 4.6 | 1.6 | 1.0 | 0.7 | 0.3 | 0.4 |
| Dense hay | 14.2 | 31.1 | 20.7 | 16.2 | 9.2 | 4.9 | 2.1 | 0.9 | 0.8 | 0.6 | — |
| Tussocks | 14.6 | 33.6 | 21.6 | 15.5 | 7.4 | 3.6 | 1.7 | 1.1 | 0.8 | 0.4 | — |
| Dense pasture | 13.9 | 32.2 | 21.8 | 17.2 | 7.3 | 3.4 | 2.1 | 1.1 | 0.7 | 0.5 | 0.4 |

Note. The fifth internode is usually the first to show green; in some of the lax hay plants, however, the sixth internode will be slightly tinged green.

Data have been presented in Tables I–VIII which afford the ground-work of the classification adopted. During the earlier years the work had not been carried far enough to permit of the accurate recognition and categorising of all the groups as presented in Table IV for 1925 and in Tables V, VI and VII for 1927. These latter tables are therefore the most informing and have also been based on data collected from the largest number of plants subjected to quantitative analyses.

It will be convenient before attempting to describe and define the several groups to examine the figures in the tables with a view to discussing the implications of the data and in order to render more intelligible the classification as finally adopted.

It will be obvious that the figures as such for yield, number of tillers and for the other characteristics brought under review cannot usefully be compared one year with another. The cuttings, weighings and counts will never have been made at precisely the same stage of growth in the different years—a few days at and about heading-flowering stage being responsible for wide differences in the characteristics under study. It is the general balance of the figures as applied to the several groups that alone has significance, and, looked at from this point of view, the data are decidedly confirmatory from season to season.

Yield. It does not necessarily follow that the types of plants having the greatest number of tillers (the most dense) are the highest yielding. There is a distinct positive correlation between height and yield—thus, on 1147 plants, representing all the groups, the coefficient of correlation was found to be $.543 \pm .041$. The dense pasture plants, though on the average of all the data having the greatest number of tillers, are not amongst the highest yielders and are not tall plants. The tussocks which have nearly as many tillers as the dense pasture plants and which are also comparatively tall are the highest yielding. Dense hay plants which are very similar in growth-form to lax hay plants, though not as tall as lax hay, are, however, very decidedly more heavy yielding and, with the tussocks, constitute the most productive plants. The coefficient of correlation between height and yield of the plants representing a single group is usually high—thus, on 150 plants of one family representing

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dense hay, it was $.693 \pm .032$. In the dense hay group, however, the leafage is well carried up the plants and the panicles do not protrude so far above the general level of the leafage (largely a function of the leafage provided by the barren tillers, which tend to be tall growing in dense hay) as in the case of tussocks, for instance, in which the "leaf up" is not as good as in hay. The coefficient of correlation for some families of tussocks was no more than $.252 \pm .032$. Within any one group the dense plants are invariably higher yielding than the more lax plants, while the same is true of whole groups in the case of closely related groups. Thus dense hay outyield lax hay, tussocks outyield cups and dense pasture usually slightly outyield spreading pasture.

Height, height/diameter and length of leaves. The hay plants constitute a very distinct group—they are usually tall—and are always tall in proportion to their girth, the ratio height/diameter generally exceeding unity. The leaves are well carried up and tend to be better lifted off the ground than in other groups. This last point is well shown by the figures in Table VIII, the fifth internode (usually the first internode to show green) contributing a higher percentage to the total height of the plant than in the case of tussocks or pasture. This is particularly well marked in the case of the extra lax plants.

Tussocks and cups are intermediate in height, while both pasture groups consist of shorter plants. The tussocks and pasture groups give a low ratio height/diameter—not so much because they are necessarily widely spreading as because they are decidedly dense. The cups vary considerably in density, but the tillers are always set at a very wide angle and thus, even in the case of lax plants, the ratio is low. Length of leaf is a very characteristic feature, hay plants always having long leaves, pasture plants short leaves, with tussocks and cups intermediate.

Seasonal growth. This is, of course, largely a function of the earliness or lateness of the plants, but constitutes a very characteristic contrasting feature as between the groups. The figures in Table VI (confirmed by those in Table III) show, however, that the hay groups (both lax and dense) make a more rapid contribution to their total height than the tussocks or pastures. The cups, which are on the average decidedly less dense than the dense hay and also slightly earlier, make more rapid seasonal growth than the dense hay group and approach most nearly to lax hay. It follows then that the groups consisting of the earlier and laxer plants make the most rapid growth—they also have the lowest percentage of barren tillers to total tillers and make the lowest contribution of leaf to total hay.

Tiller development. The most characteristic growth-form differences between the groups turn upon differential tiller development. In this connection the figures presented in Table VII are instructive. In the lax hay plants the panicle-bearing tillers all tend in the main to start elongation contemporaneously and grow uniformly together; the development of these tillers is not hampered to any very appreciable extent by the production of

barren tillers and consequently at flowering time the general level of the apices of all the panicles is comparatively similar. There will be but few late produced panicle-bearing tillers, over 70 per cent. of the total number of inflorescences falling into the highest height-class (80–100 per cent. as tall as the tallest tillers). The figures in the table show the entirely different behaviour of the pasture and tussock groups in this respect. In the dense pasture group only 18 per cent. of the panicles attain to the tallest height-class, while over 11 per cent. are only 20–40 per cent. as tall as the tallest. A comparison of the plants in Phot. 8 (lax hay) with those in Photos. 14, 15 and 16 (tussocks) illustrates the differences under review. It is interesting to note that as between lax hay and dense hay, although in many respects these groups are similar in growth-form, the density of the latter is correlated with a more uneven height distribution of the panicles than is the case in the former (see Phot. 11).

The relation of tiller formation to the general physiognomy of the plant is further shown by the figures in Table I, from which it will be seen that in the lax hay plants barren tillers formed more or less contemporaneously with the panicle tillers amount to only 13 per cent. of the total tillers, compared with 28 per cent. in the dense pasture, while the percentage of barren tillers to total tillers at full flowering time varies from about 30 per cent. to 40 per cent. according to season, compared with a variation of from about 36 per cent. to 74 per cent. in the dense pasture plants.

It is the production of contemporaneous and fast growing barren tillers that is largely responsible for the leafiness of plants at hay time, and thus it follows that the dense pasture are the most leafy and the lax hay the least leafy plants. The contribution of sheath to the hay is also a function of tiller development and tends to be high in the case of plants which produce a large proportion of barren tillers and which thus grow away contemporaneously with the panicle tillers. Thus sheath contributes 27 per cent. and 25 per cent. respectively to the hay of dense pasture and tussocks, and only 10 per cent. and 15 per cent. respectively to the lax hay and to the cups. It is the dense pasture and the tussocks in which there is the least obvious differentiation between barren and panicle-bearing tillers and in which the former at all stages make the strongest growth and the greatest contribution to the bulk of the plant. Even in dry years unfavourable to early spring growth these dense types always maintain this characteristic and maintain their density, while in the case of lax hay and the laxer of the cups the production of barren tillers will be delayed until after the plant has reached the full hay stage. The dense hay plants also tend to behave in the same direction as the other dense types, Phot. 13, comparing a dense with a lax hay plant, both grown in sand, illustrating the difference. In a similar way, the extent of the contemporaneous tiller development serves to differentiate between the lax cups and the dense cups—in the former the production of barren tillers is always deferred, while

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in the latter barren tillers are freely produced at the beginning of the growing season. A comparison between the plant shown in Phot. 22 (lax cup) with that shown in Phot. 23 (intermediate cup) and that shown in Phot. 21 (above, dense cup) illustrates this point.

In spreading pasture plants, which at flowering time will usually have as high a percentage of barren tillers as dense pasture plants early in the spring (see Tables IV and V), the density will be decidedly less than in dense pasture plants because tiller development will have been somewhat deferred.

Not only is the seasonal sequence of tiller development closely connected with the tiered or storied arrangement of the inflorescences at flowering time, but it is also intimately linked with the date of flowering and with the duration of flowering of the plants. Thus the lax hay in particular, and also the laxer of the cups, in which the panicle tillers have the longest start over the barren tillers—and which are presumably therefore not hampered by a contemporaneous production of secondary tissue—are the earliest to flower, finish flowering most quickly, and also make the most rapid spring growth. The dense pasture plants and tussocks, with their excessive contemporaneous development of barren tillers, on the other hand, are the latest to flower, tend to flower over a long period, and the dense pasture plants in particular make very slow spring growth.

The various points above noted as to tiller development are very similar in kind to the differences met with as between typical winter and spring oat varieties. The winter varieties are multi-tillering always with a certain proportion of non-panicle bearing tillers and are late. The same is true of some of the later of the spring varieties. The great majority of these latter are, however, early and slightly tillering. Thus we see that within a species of grass the tendency is for there to be a clear cut distinction between the late and early varieties and that the two groups of varieties differ from each other in particularly well-marked growth-form characteristics. These are characteristics which, although of a qualitative nature, are capable of being appraised, and when subjected to statistical study can be categorised and are moreover characteristics which, in the aggregate, affect most profoundly the general appearance of the plants.

THE VEGETATIVE GROUPS DEFINED.

In order to give precision to the data on ecotypes, to be discussed later, it will be desirable to define the six vegetative groups into which the plants have been classified in terms of the characteristics dealt with in the previous sections.

(1) **Lax hay.** These plants are usually tall with long leaves. Although in some cases the tillers start elongating at a wide angle, by the heading stage they are always more or less erect, so that the ratio height/diameter is seldom less than unity. The first internode to show green and to be definitely elongated makes a greater contribution to the total height of the plant than in the case

of other groups. It follows that the leaves tend to be lifted off the ground and the plants have the appearance of being comparatively well "leafed up." The production of barren tillers is always relatively slight and the development of these is only to a limited extent contemporaneous with that of the panicle shoots. Largely in consequence of this the plants make rapid spring growth, flower early and the inflorescences tend to be brought up to a comparatively level and uniform height. The yield per plant and the contribution of blade or lamina and of sheath to hay are low. Although narrow leaved and narrow tillered plants are met with in this group, the vast majority of the representatives tend to have broad leaves and broad tillers.

Speaking generally, there is no good connection between vegetative characteristics and panicle characteristics, but it is of interest to note that drooping panicles are not often met with in this group. This constitutes one of the most characteristic and easily recognisable of all the groups—intermediate forms between lax hay and other groups being relatively infrequent.

Typical lax hay plants (Danish) are shown in Phot. 8, lax hay plants slightly above the average in density in Phot. 9. Contrasting hay plants are shown in Phot. 11. Note the more uniform height of the panicles in the erect Danish plant (No. 1 above) than in the dense indigenous (below).

(2) **Dense hay.** Like lax hay, these plants tend to be tall, and at the heading stage have a ratio height/diameter seldom less than unity. The leaves tend to be longer even than in the case of lax hay; the first internode to definitely lengthen contributes nearly as much to the total height as in lax hay, and thus tends to differentiate the hay from other groups. The plants are well "leafed up" and always have the appearance of surpassing lax hay in this respect.

The dense hay plants are multi-tillering with a high percentage of barren tillers, a very large proportion of which are "early produced" and grow away contemporaneously with the panicle tillers. The panicles therefore tend to be more aggregated into tiers than in the case of lax hay. The contribution of blade or lamina and of sheath to the hay is also higher. The dense hay plants are among those giving the highest yield. The dense hay plants are as late in flowering as the spreading pasture, but although late they make more rapid spring growth than any other of the dense groups, though in this respect they fall far short of the lax hay.

A considerably larger proportion of narrow leaved and narrow tillered plants are met with in this group than in lax hay plants with these characteristics being most abundant in dense hay and dense pasture.

Drooping panicles are fairly frequent in this group, but Classes II, III and IV are the most abundantly represented.

The dense hay group tends rather to merge into the tussock group as the plants become less tall, somewhat more spreading and with the leaves carried less well off the ground.

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Typical dense hay plants are shown in Photos. 6 and 7. Note that in these plants panicle exertion has not commenced or is only slightly in evidence while it is far advanced in the lax hay plants (see Phot. 8). Compare also Phot. 11, contrasting dense with lax hay under normal conditions, and Phot. 13, contrasting the two types when grown in sand. Intermediate plants between lax and dense hay with excess of panicle tillers are shown in Phot. 12.

(3) **Tussocks.** All the representatives of this group are dense, and intermediate in height between the hay and pasture groups. The leaves are long—as long as those of lax hay.

The tussocks are characterised by excessive tiller production and a considerable contemporaneous development of barren tillers which tends to cause a markedly tiered arrangement of the inflorescences, this being more in evidence in the tussocks than in the hay groups or the cups, and gives rise to high yielding plants with a high proportion of sheath to the total bulk. On the average of the data for all seasons the tussocks must be regarded as the highest yielding group and this is also confirmed by field plot trials.

The tussock plants may be erect or wide spreading—in the case of the spreading plants the wide inclination of the panicle tillers is somewhat obscured by the contemporaneous and abundant production of barren tillers which fill up the body of the plant. The ratio height/diameter is always considerably less than in the case of typical hay plants, while the first internode to be elongated makes but little, if any, greater contribution to total height than in the pasture plants. The tussocks are late flowering on the average, slightly later than dense hay and nearly as late as the pasture groups—they grow more rapidly than the pasture plants but not as rapidly as the dense hay. Broad and narrow leaved plants are about equally represented in this group.

Drooping panicles are decidedly infrequent amongst the tussocks, Classes II, III and IV being the most abundantly represented. The tussocks tend to merge on the one hand into dense hay and on the other into cups (see "Cups" below).

Typical tussocks are shown in Photos. 14, 15 and 16. Note the markedly tiered vertical distribution of the apices of the panicles and the extreme density of the plants.

A plant somewhat intermediate between tussocks and dense pasture is shown in Phot. 21 (No. 1, below).

(4) **Cups.** These constitute a large and somewhat variable group, the main characteristic of which is the excessively wide inclination of the early produced panicle tillers. In extreme cases such tillers are but little lifted off the ground right up to the heading stage, and at the heading stage always maintain a very wide angle; thus the ratio height/diameter independently of the degree of density of the plant is of necessity low—much lower than in the case of the hay and tussock groups. Early in the spring it is always the

widely inclined butts of the panicle tillers that give the typical cup-shaped appearance to these plants; it is only when the barren tillers are abundantly produced and tend to cover over the butts of the panicle tillers that the extreme openness of the plants is to some extent masked. Contemporaneous production of barren tillers is always less abundant than in the case of tussocks, but in the denser plants the contribution of these at the heading stage may be relatively high. On the average of the group as a whole, however, it is nearly as low as in the case of lax hay (see Table V).

The cups are of two distinct types "lax" and "dense," the former in many respects come close to lax hay—they flower relatively early, tend to develop barren tillers only late in the season and produce a hay with a low percentage of leaf and of sheath.

The dense cups are high yielding and approach very close to tussocks. The production of barren tillers may be considerable, but generally commences later in the season than in the case of typical tussocks. In a dry year the differentiation between dense cups and tussocks is comparatively easy since as well as ratio height/diameter the more delayed tiller development of the cups is exaggerated; in a wet year the ratio height/diameter has to be more completely relied upon. It is probable therefore that in the grouping here adopted there has been more overlapping in respect of dense cups and tussocks than in the case of other groups.

Semi-erect panicles appeared to be slightly more prevalent in this than in other groups, drooping panicles are seldom met with.

The general growth habit of the cups is shown in marked contrast with erect hay in Phot. 10. A large and late dense cup is shown in Phot. 21 (above), a medium early dense cup in Phot. 18 (No. 2, above), and an early semi-dense cup in Phot. 18 (below). A lax and early cup with few barren tillers is shown in Phot. 22, while one with a considerable number of barren tillers is shown in Phot. 23.

Pasture types.

The two pasture groups are characterised by the plants not being tall and having relatively short leaves, and by a low ratio height/diameter. The ratio is here affected rather by the extreme density of the plants and the shortness of the flowering tillers than by the wide inclination of the tillers. The first internode definitely to elongate makes only a slight contribution to the total height of the plant.

Pasture plants are not heavy yielding, simply because they are not large compared with dense hay and tussocks.

(5) **Spreading pasture type.** This group includes several fairly well defined types which for the present purpose are conveniently brought together in a single group.

The spreading pasture plants are decidedly less dense than the dense

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pasture plants, largely owing to the fact that a considerable proportion of the barren tillers are developed subsequent to the elongation of the panicle shoots. Some of the spreading pasture plants have widely inclined panicle tillers and start rather as miniature cups, but fill up more completely and more rapidly than the latter, while they tend to be later to flower and consequently have their panicles at flowering time more evenly distributed over the height classes, and they also grow more slowly early in the spring. The contribution of blade or lamina and of sheath to the hay is higher than in any group except dense pasture. The "leaf up" in these plants is generally very low, the panicles being carried high above the general leafage.

A very typical sub-group of spreading pasture is characterised by the flatness of the plants—the general outline being neither convex (like dense pasture or tussock) or concave (like cups). In these plants the panicle tillers are not widely inclined and even in the earliest stages do not tend to form a cup. The flat distribution of the leafage is due to the fact that the barren tillers all tend to grow away together, and do not differ in height or inclination amongst themselves to the same extent as in dense pasture, in which the central tillers are more erect and longer than the marginal ones. In the main the spreading pasture plants tend to be broader leaved and broader tillered than the dense pasture.

All types of panicles are met with amongst the pasture plants.

Typical spreading pasture plants in contrast with dense pasture are shown in Photos. 17, 19 and 20.

(6) **Dense pasture type.** This is a very characteristic group having many of the attributes of tussocks in miniature. The plants are, however, more sharply convex in outline and even denser than tussocks with a higher proportion of barren tillers. The inflorescences are very markedly aggregated into tiers, only 18 per cent. falling into the tallest height class, while nearly 13 per cent. (compared to 0.3 per cent. in the case of lax hay) attain to a height of less than 40 per cent. of the tallest panicles. The contribution of blade or lamina and of sheath to the hay is higher than in any other group and the plants make particularly slow growth in the spring.

In general these plants have the appearance of being comparatively erect—the panicle tillers, at all events seldom, being widely inclined.

The barren tillers tend, however, to be erect towards the middle of the plant and more inclined outwards from the centre. Although a large proportion of the barrens grow away contemporaneously, with the panicle tillers new barrens are continuously developed: thus at the heading stage the plants are excessively dense. Owing to a large proportion of the barrens growing up with the panicle tillers, the leafage has the appearance of contributing well to the total height of the plant.

The plants of this group are the latest to flower; individual plants are however occasionally met with which, although having all the growth-form

characteristics of the group as a whole, none the less flower comparatively early.

Narrow leaved and narrow tillered plants are abundantly met with amongst the dense pasture group. Plants with very few panicles at flowering time are not infrequent in both the dense and spreading pasture groups, such plants failing to develop panicles in normal amount year after year.

Typical dense pasture plants in contrast with spreading pasture are shown in Photos. 17, 19 and 20. An early dense pasture plant is shown in Photo. 18 (No. 1, above) while types of pasture plants bearing very few panicles are shown in Photo. 24.

GENETICAL STABILITY OF THE GROUPS: SELF- AND CROSS-FERTILITY AND VIGOUR.

Cocksfoot is a highly cross-fertile plant, but is by no means self-sterile. During the course of the investigations under review 250 mother plants have been selfed and of this number only 14, or 5.6 per cent. have failed to set seed. The amount of seed set is, however, usually very slight, but in an appreciable number of plants the seed setting may be nearly as good as when cross-fertilisation is allowed full play. The following statement will serve to illustrate the general behaviour of the plants¹.

| Percentage of total number of plants selfed (during period 1921-25) which fall into the various fertilisation categories | Fertilisation categories |
|---|---|
| 3.6 | Up to average standard of cross-fertilisation |
| 0.6 | About 75 per cent. of cross-fertilisation |
| 4.0 | About 50 per cent. to 75 per cent. of cross-fertilisation |
| 10.8 | About 25 per cent. to 50 per cent. of cross-fertilisation |
| 22.2 | About 5 per cent. to 25 per cent. of cross-fertilisation |
| 53.2 | Less than 5 per cent. of cross-fertilisation |
| 5.6 | Failed to set any seed |

It follows from the above statement that it would seem reasonable to suppose that the vast majority of plants of cocksfoot met with in natural and semi-natural habitats would be of hybrid origin—would in fact represent F_1 plants. It is however more than probable that quite an appreciable number of such plants may be the result of selfing and may therefore represent an F_2 or subsequent generation. It should be stated further that quite an appreciable number of F_3 plants selfed to produce F_4 have given practically as much seed as F_1 plants allowed to inter-pollinate.

The present paper is not the place to enter into detailed genetical considerations; but in connection with the question of ecotypes it is necessary

¹ The above is of course a generalised statement and is based on the average number of viable seed per panicle resulting from bagging the panicles of two unrelated plants together. This figure is taken as the standard of cross-fertilisation to which the selfed plants are compared. The influence of bagging as such has therefore been the same in both cases. Plants giving high seed yields have been re-bagged in a subsequent year and have again produced an abundance of seed.

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to have some correct picture of the potentialities of our species in relation to both cross- and self-fertility and cross- and self-vigour¹.

F_2 to F_n plants are not likely to be met with to any appreciable extent under natural and semi-natural conditions unless such plants are not only produced in moderate quantity but are also reasonably vigorous. It is quite out of the question here to review the detailed evidence that has been collected: a large number of families now having been taken to the F_4 generation. On average figures vigour undoubtedly falls off from F_1 to F_4 and is frequently very marked in F_2 . Cocksfoot is, however, considerably more self-vigorous than is perennial rye-grass, for instance; not only is this so when judged by average figures but what is of greater interest in the present connection is the fact that a very appreciable number of cocksfoot plants, when selfed generation after generation (F_1 to F_4), give progeny plants in F_4 which are highly vigorous, in certain cases practically as vigorous indeed as the original (presumably) F_1 plants. The inheritance of vigour is, of course, largely a matter of segregation, but it is of particular interest to note that in numerous cases, when the most vigorous plants in an F_2 family are selfed, the average of vigour in the resulting F_3 and F_4 is perfectly well maintained. It will be realised that it is difficult critically to compare vigour generation after generation unless at all stages plants are re-selfed so that the various generations can be grown contemporaneously and side by side for accurate quantitative comparison.

The extent to which considerable vigour *can* be maintained—and that is all that it is necessary to demonstrate in the present connection—is sufficiently shown by the following facts.

The experimental block of 1927 was a large one and contained characteristic plants in F_1 , F_2 , F_3 and F_4 —lax hay and dense cups being particularly well represented. All the plants had been treated similarly and were growing in close proximity to each other and were of precisely the same age. In the case of lax hay the number of plants in each generation was sufficient to allow of good comparisons in yield. The F_1 were Danish plants grown direct from commercial seed, the F_2 , F_3 and F_4 also came from Danish plants, but were not the lineal descendants of the plants now growing on the block—nor were the F_2 , F_3 and F_4 plants lineal descendants from each other. The plants in each generation were, however, lineal descendants from lax hay plants—and in each generation the most vigorous plants had been selected for selfing. The plants were cut and weighed in the hay stage (July 10th) and gave the following average green weights (in oz.):

| | F_1 | F_2 | F_3 | F_4 |
|--|-------|-------|-------|-------|
| Weight per plant | 11.3 | 10.1 | 8.9 | 8.8 |
| Number of plants | 244 | 335 | 297 | 517 |
| Weight per plant of the 20 heaviest plants | 16.3 | — | — | 14.1 |

¹ This aspect of the general question will be dealt with in detail elsewhere in a subsequent paper and nothing would be gained by here reviewing the extensive literature on the subject.

In this connection no account has been taken of seedling or young plant casualties, but only of plants which had survived to the hay stage of the second harvest year—in many cases, however, this being 100 per cent. of the individuals originally planted out in 1925.

The above comparison is, of course, not absolute or critical, chiefly because the original F_1 plants that were selfed had been selected for vigour and would certainly have been higher yielding than the average of the 244 plants here considered, but even if the F_1 figure is taken at 16.3 (the average of the 20 heaviest yielding plants) and compared to the average figures for all the plants in the F_2 , F_3 and F_4 generations it will be seen that the vigour has still been well maintained. The heaviest weight of F_1 plants were about 20 oz., several of the F_4 plants also attaining to weights exceeding that figure.

The evidence obtainable from dense cups is in a similar direction, six out of 90 F_1 plants gave yields in excess of 20 oz., while two out of 50 F_4 plants also produced over 20 oz. of green fodder. The point of interest chiefly to be noted is that when selecting at every stage for vigour, in each generation plants, practically as vigorous as typical and highly vigorous F_1 representatives of the several groups, will be freely encountered, and that the average of vigour in F_4 is, under these conditions of selfing, apparently sufficiently high to warrant the expectation that under competitive influences an appreciable number of plants should be able to survive even if growing on the same habitat and in the closest association with normally produced F_1 individuals.

It has then been sought to show that individual plants of cocksfoot *can* produce a relative abundance of seed under selfing, and that such seed in certain cases is *able to produce* a large proportion of highly vigorous plants, and that this state of affairs *can be* maintained to the F_4 generation.

It would almost necessarily follow that this potentiality for self preservation under enforced selfing has been operative in nature and under certain sets of conditions undoubtedly a factor to be seriously reckoned with in connection with ecotypical selection.

BREEDING TESTS ON THE GROUPS.

Large numbers of plants representative of all the groups have been carried (by selfing) to F_3 and smaller numbers of some of the groups to F_4 . These tests cannot at present be regarded as final, because in the first place the number of plants brought under test has not been nearly sufficient, and in the second place because it has not yet been possible to estimate precisely the effect of loss of "vigour" on the phenotypical physiognomy of the progeny plants. Loss of vigour, as above pointed out, does not necessarily occur in successive generations, but it is the most usual happening. The characteristics of the groups, as above explained and defined, are largely a function of tiller development, and all the evidence would seem to suggest that tiller development is profoundly influenced by vigour, no matter whether that "vigour"

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is "inspired" by inherent strength and hampered by inherent weakness or, on the other hand, is inspired or hampered by favourable or adverse environmental conditions (soil fertility, for example). It may well be therefore that certain progeny plants would fall into phenotypical groups to which genotypically they do not properly belong—that is to say, they might fall into a particular group simply because the conditions have not favoured the revelation of their full potentialities—lack of vigour and not segregation to a different entity being perhaps all that is involved. The data presented in Table IX, although far from complete, throw some preliminary light on the question and also show that the groups would seem to vary considerably one from another in the character of breeding true to their class.

Table IX. *Showing for each of five (vegetative) groups of cocksfoot the distribution of the progeny plants in F_2 , F_3 and F_4 respectively in the six vegetative groups that have been recognised or defined. The figures represent the percentage contribution to each group. 1923–1926.*

| Groups into which the mother plants were assigned | | Groups into which the progeny plants were assigned | | | | | | Number of progeny plants contributing to each |
|---|-------|--|-----------|------|----------|-------------------|---------------|---|
| | | Lax hay | Dense hay | Cups | Tussocks | Spreading pasture | Dense pasture | |
| Lax hay | F_2 | 96.0 | — | 3.5 | — | 0.5 | — | 198 |
| | F_3 | 86.0 | — | 9.5 | — | 5.0 | — | 100 |
| | F_4 | 85.5 | 0.5 | 10.5 | 2.0 | 1.5 | — | 199 |
| Dense hay | F_2 | 21.0 | 34.0 | 28.0 | 7.0 | 10.0 | — | 756 |
| | F_3 | 30.0 | 8.0 | 40.0 | 4.0 | 17.0 | — | 230 |
| | F_4 | 29.0 | 59.0 | 12.0 | — | — | — | 17 |
| Cups | F_2 | 3.2 | 2.4 | 70.6 | 12.7 | 11.1 | — | 126 |
| | F_3 | 1.0 | 2.0 | 90.0 | — | 7.0 | — | 101 |
| | F_4 | 28.0 | — | 54.0 | 4.0 | 14.0 | — | 71 |
| Tussocks | F_2 | 4.2 | 5.7 | 43.6 | 40.2 | 6.3 | — | 142 |
| | F_3 | — | — | — | — | — | — | — |
| | F_4 | — | — | — | — | — | — | — |
| Pasture | F_2 | 5.3 | 2.1 | 40.3 | 0.7 | 49.0 | 2.6 | 431 |
| | F_3 | 10.3 | 7.3 | 27.3 | 5.5 | 33.2 | 16.4 | 55 |
| | F_4 | — | — | — | — | — | — | — |

It will be apparent from the figures in the table that on the face of it "lax hay" and "cups" breed remarkably true to type. It will also be noted that, taking all the groups together, there appears to be a strong tendency in favour of segregation towards cups. The cup type of growth-form is however closely associated with lack of vigour and failure to produce contemporaneous barren tillers. Observations amongst the experimental plants in relation to soil heterogeneity have revealed the fact that on poorer or water-logged patches of soil plants which do not properly belong to this group are prone to assume the characteristics by which its true representatives are recognised.

The breeding work as a whole goes to show however that true "cups," i.e. plants possessing the power of producing this growth-form only, are

perhaps the most plentiful representatives of the species *Dactylis glomerata*; and consequently, although in F_2 , F_3 and F_4 the phenotypes assigned to this group are almost certainly somewhat in excess of the number that have segregated to true cups none the less under segregation, the balance of the specific characters inevitably tends in that direction. This perhaps suggests that cups represent a growth-form—a phenotype—that manifests itself from devious genetical constitutions. It remains a fact, however, that it is amongst lax hay and cups that the greatest number of plants breeding absolutely true to type have been met with; and in the main these groups, particularly lax hay, must be regarded as highly stable both phenotypically and genotypically.

Dense hay appears to segregate strongly towards lax hay and cups, but it is highly probable that a very appreciable number of the segregates assigned to these two lax groups are so assigned because of loss of vigour. In this connection it is interesting to observe that occasionally a dense hay plant is encountered which breeds absolutely true to the group characteristics of dense hay—a plant which under selfing maintains its vigour. Thus, too, it is seen that in F_4 (when it has been always the most vigorous previous progeny plant that has been selfed) the number of dense hay segregates has been increased. That vigour has much to do with the outward and visible manifestation of dense hay plants is further suggested by the fact that when two or more typical dense hay plants are caged together to interpollinate the progeny conform much more closely to dense hay than when single plants are selfed. Thus the progeny (500 plants) of three plants so caged gave 60 per cent. dense hay, 29 per cent. lax hay and 11 per cent. cups. In the case of three plants of lax hay caged in a similar manner the whole progeny consisted of true lax hay plants, thus further emphasising the genotypical purity of the lax hay group.

Of all the groups the tussocks would appear to be the least true breeding; but, as before explained, it is not always easy to differentiate accurately between tussocks and cups. Even so, however, this group is the only one from which no single truly representative plant has been obtained which when selfed breeds absolutely true to growth-form characteristics. This fact may be purely a matter of vigour or it may be that the tussocks constitute essentially hybrid and highly heterozygous phenotypes. Relatively pure breeding progenies are obtainable from caging vigorous plants of seemingly identical type together for inter-pollination.

The pasture groups like the dense hay appear to segregate towards the laxer types, particularly towards cups, but breed more truly than do the dense hay. This is not only shown by the average figures but by the fact that more pasture plants have bred absolutely true to type than have dense hay. The flat type of spreading pasture are prone to breed decidedly true, several such plants having given absolutely pure F_2 and F_3 progenies—typical dense

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pasture plants do not breed so true, but we now have a few true breeding families in F_2 .

Taking the data as a whole, it would seem justifiable to assume that the groups as defined, and based as they are on phenotypical criteria, have a decided genotypical significance—for although segregation occurs within every group, as is only to be expected in a highly cross-fertile species, yet the trend of segregation is peculiar to each group as such. At the one end of the scale we have the early and lax hay group breeding remarkably pure and giving rise to only a very small proportion of pasture segregates, and at the other the pasture group giving rise predominantly to pasture and cup segregates (many of the latter being probably due to lack of vigour) with but a small proportion of lax hay plants. It is only pasture plants which give segregates conforming to the dense pasture group, and to a really high proportion of plants belonging to the spreading pasture group. Both dense hay and cups, however, give rise to an appreciable number of spreading pasture segregates. Tussocks do not segregate out of any of the other groups to any considerable extent and are perhaps the least true breeding of all the groups.

BREEDING TEST OF PANICLE CHARACTERS.

Although no breeding tests have been set up with the main purpose of investigating the inheritance of panicle character, Dr Davies has examined a number of the families that have been grown for the study of vegetative characteristics from the point of view of their panicles also. In the main, families in F_4 breeding true or practically true to vegetative group class appear also to breed relatively true to panicle character. This is strikingly the case in respect of mother plants having panicles representative of Class II and Class III. The majority of the lax hay plants with these types of erect panicle have given progenies showing a purity of 85 to over 90 per cent. In several of these families only one out of 23 progeny plants has departed from uniformity in panicle character. This and other evidence suggests that plants with erect and compressed or semi-compressed panicles are less heterozygous than those with spreading panicles. The data as a whole also tend to emphasise the relatively true breeding propensities of the lax hay plants considered as a biologic group of the species.

THE GROUPS IN RELATION TO HABITAT: ECOTYPICAL SELECTION.

As before explained, this study has not been concerned with ultra-characteristic habitats and therefore it is not to be expected that single well marked ecotypes should be associated with the types of habitat here under review. That such definite ecotypes do exist in the case of *Dactylis glomerata* is, however, suggested by Turesson's conclusion that the var. *lobata* is a

hereditary shade variety; while evidence from the present work is not lacking to suggest that other very definite ecotypes occur within the species.

Three main types of habitat are here to be considered, each very largely the outcome of the activity of man. These are (1) temporary leys, (2) old swards, and (3) waste places, hedges and thickets. It will be desirable briefly to discuss, in the light of agronomic investigations in progress at the Welsh Plant Breeding Station, the main factors presumably affecting ecotypical selection which these habitats superimpose upon the plants contributing to their colonisation.

(1) *Temporary leys*. The cocksfoot seed harvested in Denmark and much of that harvested in the United States of America is taken in the first and second harvest years from temporary leys. In Denmark the crop is grown for seed from specially prepared seed production drills. These conditions allow of infinite scope for the production of inflorescences and for cross-pollination, since the crop is always "shut up" early for seed and the seed-producing plants form one continuous mass. The crops are not grazed hard early in the spring. The conditions are therefore such as to encourage the early and rapid growing strains which, because they are not grazed back when making vigorous growth, are allowed maximum smothering effect on the slower and late growing strains. By growing in drills this favouring of the early strains is the more accentuated since growth tends to start earlier than in sward; and consequently the later strains tend to be the more completely shaded. It has been shown by repeated trials at the Station that the late strains establish themselves more slowly than the early and do not do themselves as full justice in a first harvest year as do the early. The plants developed on a sward in the first harvest year owe everything to the seed sown and therefore to the powers of establishment of that seed. Large seed of high viability has been shown by Davies (3) to establish itself better than small seed, while Stapledon (7) has shown that the earlier strains of a species tend on the average to have larger seed than the late. The earlier strains are therefore given an initial advantage over the later, independently of subsequent conditions further favouring the early. Any processes of selection that may be at work are rapidly augmented by the fact that in seed-producing districts the seed from one temporary ley is used to sow out the next—the influences of practice are therefore cumulative.

(2) *Old swards*. Cocksfoot is not usually a very abundant grass on really old swards (such as, for example, the Leicestershire and Northamptonshire fattening pastures). The plants do not therefore form a continuous mass; under conditions of heavy grazing, moreover, the plants do not run excessively to inflorescence, so that scope for cross-pollination is relatively limited. Re-establishment from self sowing from the comparatively small amount of seed that may be annually produced is not easy on a dense sward. It would therefore follow that the cocksfoot plants inhabiting an old grazed sward

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would be likely to owe their presence chiefly to an ability to withstand the conditions, since the opportunities for repeated re-introduction are so obviously limited. It has been proved at the Station (see, for instance, Stapledon (8)) that it is the late and multi-tillering strains that best withstand repeated and heavy defoliation and that, when once introduced on to a grazed sward, have the greatest ability for maintaining themselves.

(3) *Waste places, hedges and thickets.* These habitats have much in common; they are not grazed to any extent, so that the continued operation of the grazing animal is unable to exert any selective influence, and the plants if cut back are frequently not so cut until much ripe seed has had an opportunity of being shed. Seed that is shed does not fall on a dense sward and there are moderately good opportunities for repeated self-establishment. The plants grow abundantly and fairly close together, so that opportunities for cross-pollination are ample. The plant population does not, however, develop into such a dense canopy as is formed when a temporary ley in an early harvest year is put up to seed: consequently the earlier and quicker growing varieties cannot be expected to exercise the same retarding and finally eliminating influence on the later and slow growing.

DERIVATIONS OF THE THREE MAIN HABITAT CONDITIONS.

Closely related to the above main habitats for cocksfoot are (1) meadows, and (2) the somewhat exceptional conditions met with on the seed-producing areas on the Banks Peninsula and in the Canterbury Plains of New Zealand.

Old meadows. On meadows the sward is not as dense as on old pastures, the plants are given every chance to flower freely and to inter-pollinate; and moreover since the tendency always is to cut hay too late there will be at least in some years considerable opportunities for continued self-establishment by seed shedding. Hay crops are, however, usually not "put up" as early as seed crops, consequently heavy grazing early in the spring, year after year, may be expected to exert a cumulative influence somewhat in favour of the late multi-tillering and adverse to the early strains.

The Banks Peninsula (Akaroa district) and Canterbury Plains, New Zealand. The conditions obtaining on these interesting cocksfoot habitats have been fully discussed in a recent article by the present writer (Stapledon (9)), and it is only necessary here to state that in general the influences affecting selection are more akin to those met with on the waste place types of habitat than on temporary leys, old swards, or on meadows as understood in this country.

OTHER HABITATS.

Cocksfoot is often a very successful coloniser on the exposed cliff tops facing the Atlantic. Considerable closed associations of this species are to be met with on the Welsh coast and on that of North Devon and North Cornwall. Such areas are usually but slightly grazed if at all. These habitats must be

deemed to be critical and, one would suppose, adverse to re-establishment from self seeding, and particularly adverse to plants beginning to make active growth too early in the spring. The areas are continually swept by gales and high winds, frequently accompanied by heavy rainfall. The conditions would therefore be expected to be adverse to fertilisation and adverse to the maturing of seed of high viability—often, indeed, it must be the fate of the pollen when shed to be carried away by the wind far from the plants colonising these exposed situations.

DISCUSSION OF THE EVIDENCE.

A broad survey of the actual relation of the types (vegetative groups) of cocksfoot contributing to the chief habitats under review is rendered possible by reference to the data presented in Table X.

Table X. *Showing (1) the distribution of cocksfoot plants from different sources of origin (habitats) amongst the chief vegetative (phenotypical) groups into which the species has been classified, (2) the relation of height to source of origin, and (3) the relation of flowering date to source of origin. 1920-27.*

| Nationality and source of origin | Percentage contribution to the vegetative groups | | | | | | Percentage contribution as to height | | Percentage contribution as to flowering date | | | |
|---|---|-------|-----------|-------|-----------------------|-----------------------|--|----------------------------|---|-------------|---------------------|------|
| | Hay types | | Cup types | | Tus- sock types | Pas- ture types | Over 100 cm. | Less than 100 cm. | Early | Me- dium | Me- dium late | Late |
| | Lax. | Dense | Lax. | Dense | | | | | | | | |
| U.S.A. | 51 | 8 | 31 | 5 | 2 | 3 | 78 | 22 | 40 | 50 | 9 | 1 |
| Danish | 58 | 8 | 28 | 3 | 1 | 2 | 78 | 22 | 61 | 32 | 6 | 1 |
| New Zealand | 20 | 11 | 13 | 30 | 17 | 12 | 27 | 73 | 25 | 35 | 32 | 8 |
| Indigenous from hedges and thickets | 11 | 15 | 15 | 20 | 25 | 14 | 31 | 69 | 17 | 35 | 34 | 14 |
| Indigenous from old meadows* | 11 | 17 | 18 | 16 | 26 | 12 | — | — | — | — | — | — |
| Indigenous from Leicester- shire, Northamptonshire and Romney Marsh | 4 | 8 | 10 | 16 | 10 | 52 | 24 | 76 | 4 | 32 | 48 | 16 |
| Indigenous from other old pastures | 3 | 12 | 6 | 17 | 6 | 56 | 15 | 85 | 11 | 35 | 38 | 16 |

* Only based on 50 plants: all the other sources of origin based on over 200, and in several cases on over 2000 plants each.

The results are of extreme interest and show, for example, that under the temporary ley conditions of Denmark and the U.S.A. the seed harvested gives rise predominantly to the lax and early types of the species, while from the old Leicestershire and other swards the plants are as predominantly dense and late. These two man-made habitats represent the two extremes of conditions, the species having adjusted itself to the one by developing excess of lax hay types and to the other by virtue of colonisation by pasture and other dense and in the main late forms. It is thus seen that the ecotypical adjustment in respect of these habitats is precisely what would have been expected from an examination of the conditions superimposed by each. The temporary

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leys are peopled by the early and relatively short-lived strains and the old swards by the late and relatively long-lived strains: conditions long continued favouring each respectively have exercised an ecotypical selection of the types best able to survive the conditions.

Intermediate between these extremes of habitat we have the waste place, hedge, meadow, and New Zealand conditions, each giving rise to a population of plants of very similar group distribution—populations in general character intermediate between those of the temporary leys on the one hand and the old swards on the other. In view of the fact of the general similarity between the Akaroa habitat of New Zealand and that of waste places, it is particularly interesting to find the distribution of types so very similar under the two sets of conditions. In this connection it is also of significance to note that 40–60 years ago, when cocksfoot was first sown on the Banks Peninsula, the character of the seed then going to New Zealand would not have been of the modern (temporary ley grown) Danish type, but would rather have represented seed largely collected from waste places in Europe. The fact that waste place populations contain the most even distribution of the several vegetative groups, including a fair proportion of both lax hay and of dense pasture types, also accords with expectation, the evidence, as a whole, from an examination of the several populations, being in marked agreement with the estimate of the various habitats as above outlined, thus indicating that the estimate evidently represented a true picture of the more important factors influencing type selection.

PARTICULAR HABITATS.

The fattening pastures. A large amount of material has been collected from the fattening pastures (Leicestershire, Northamptonshire and Romney Marsh), careful notes, supported by historical evidence given by the occupiers, having been made on the fields from which all the plants were collected. The data resulting from these collections are set out in Table XI.

The oldest and best fields with dense swards upon which seed development is at a minimum will be seen to contain a preponderant proportion of pasture (dense multi-tillered) types. On younger fields and on such as have been periodically “put up” to hay the pasture types are less abundant (only 37 per cent.), while lax and early forms contribute as much as 45 per cent. to the total population.

The fact that the types are not accidental growth-forms due to local differences within the several fields is abundantly proved by Part II of the table, which gives particulars of the progenies from selfing the plants that were actually dug up. The pasture plants, whether dug up from the very best or from the less typical fields, have given families consisting predominantly of pasture and dense plants, in each case no more than 5 per cent. of the progeny population representing early and lax types.

Table XI. Showing (1) the distribution in the vegetative groups of the plants collected from the oldest and best of the Midland fattening pastures compared with fields relatively younger, or in close juxtaposition to arable fields and temporary leys, and (2) the behaviour under segregation (when selfed) of the plants collected from the different fields. 1925-27.

| The character of the fields | Percentage contribution of the plants in the vegetative groups | | |
|---|---|---------------------------------|---------------|
| | Lax and (or) early types | Tussocks and (or) dense cups | Pasture types |
| I. <i>The original plants as dug up</i> | | | |
| From the ten oldest and best fields | 20 | 7 | 73 |
| From four fields relatively young and or near arable fields | 45 | 16 | 39 |
| II. <i>First generation segregates from the plants as originally dug up</i> | | | |
| (a) The best and most typical pasture plants selfed: | | | |
| Typical pasture plants taken from the oldest and best fields | 4 | 9 | 87 |
| Typical pasture plants taken from the relatively younger or near arable fields | 5 | 13 | 82 |
| (b) In the case of early or lax plants other than those representing the pasture groups selfed: | | | |
| Plants taken from the old fields* | 43 | 43 | 14 |
| Plants taken from the younger fields* | 36 | 62 | 2 |

* Only based on 50 segregates in each case. All the other figures based on groups of 200 to 450 plants respectively.

Lax and early plants taken from both the older and younger swards when selfed have, on the other hand, given progeny populations with relatively few pasture plants and with excess of early and lax forms, together with (as would be expected from the selfing evidence previously discussed) a large proportion of cup types.

The fact that the lax and early plants taken from the oldest and best pastures have given more "pasture" segregates than those taken from the poorer and younger fields suggests that on the latter there may have been more out-crossing between the different types.

Within the pasture groups various interesting types are to be found. A good example of such a type is illustrated in Phot. 20 (No. 2). These plants are small but particularly dense and narrow leaved and are usually amongst the latest to flower, frequently producing very few panicles (see Phot. 24, No. 1). This "ecotype" has so far only been met with on the oldest and densest pastures (i.e. on some of the fattening pastures), on very old commons and other swards known to have been in grass for upwards of 100 years. It is, however, relatively infrequent and never constitutes the only or even the predominant sub-type on any particular sward. Some plants of this type immediately breed true in F_2 , others segregate to other pasture and cup types.

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Sea cliffs. A number of populations from the cliff habitats previously described have been examined. Plants taken from near Tintagel proved to be wonderfully uniform in representing the dense pasture type—the plants, however, being extra dense with unusually short and rigid leaves. Typical plants selfed gave rise chiefly to dense pasture and cup types.

Some of the sea cliff populations examined have consisted wholly of dense cups, plants which on being selfed have bred almost absolutely true to the characteristics of the mother plants.

Thickets and waste places. A large number of these populations have been examined in detail. The pasture types met with are chiefly representative of the “spreading pasture” group, and it is spreading pasture plants that are also the commonest pasture representatives on old meadows. Such plants are very abundant on the oldest swards and also appear to contribute more to the pastures of some districts than of others—they are, for example, more abundant on the cow pastures of the Aylesbury district than on the Leicestershire pastures. A number of striking types have been noted, most of which tend to breed remarkably true in F_2 .

The thickets are rich in dense hay types and in tussocks, and the largest and heaviest yielding plants have usually been obtained from such habitats.

FACTORS RESPONSIBLE FOR ECOTYPICAL SELECTION.

The evidence discussed would seem to show that two main factors tend to make ecotypical selection a biologic possibility, and that influences working differentially on these factors make for the relative dominance of one type of plant or another on particular habitats. The decisive factors are opportunities for (or natural barriers to) cross-fertilisation and the power of establishing the perennial habit.

It will be apparent from the figures given in Tables I, III and IV that the scope for inter-pollination between the extreme lax hay types and the pasture types is very limited, since contemporaneous flowering of plants representative of the two types occurs only to a negligible extent. The limit set to free inter-fertilisation between plants of different types and different flowering dates is probably more severe than is generally realised, for, as Jenkin (6) has shown, the more often the stigmas of a plant are dusted with the pollen of the potential male parent the greater is the likelihood of successful fertilisation. It would follow therefore, that if the zenith of flowering of one plant was only a day or two removed from the zenith of flowering of another, the chances of cross-pollination would not be as great as if both plants attained their zenith on the same day.

The chances of inter-pollination would seem, however, to be influenced not only by the date of flowering but also by the time of day of flowering. Dr Davies (2) has shown that individual plants tend to exert their anthers at approximately the same time morning after morning, some plants doing

so at about 5.30 a.m. and others not until 8.30 a.m.—at Aberystwyth all plants bloom early in the morning. The remarkable uniformity of flowering time is indicated for 14 plants by the figures in Table XII¹. Very similar results have been reported by Wolfe (13) in America where, although flowering lasted over a longer period each day, 77 per cent. of the plants bloomed between sunrise and noon. It is thus evident that within a readily cross-fertile species very considerable natural barriers exist to the indiscriminate hybridisation between all types of plants representing that species, and this is very largely the cause of the clear cut distinctions met with between the early and late strains of most of our herbage species.

Table XII. *Showing times of anther exsertion of 14 plants on four days. 1925.*

| Station number of plant | Times of anther exsertion on | | | |
|----------------------------|------------------------------|-------------------|-------------------|-------------------|
| | June 11th a.m. | June 12th a.m. | June 13th a.m. | June 15th a.m. |
| 318 (1) | — | 5.29 | 5.33 | 5.31 |
| 318 (3) | 6.2 | 5.57 | 5.59 | — |
| 318 (4) | 6.4 | 6.0 | 5.59 | — |
| 318 (1) | 6.44 | 6.41 | 6.44 | — |
| 322 (1) | 6.47 | 6.46 | 6.48 | 6.45 |
| 341 (1) | 8.12 | 8.14 | 8.10 | — |
| 450 (5) | — | 6.6 | 6.6 | 6.3 |
| 517 (4) | — | 6.53 | 6.50 | 6.46 |
| 647 (5) | — | 7.6 | 7.3 | 7.2 |
| 654 (4) | 6.13 | 6.15 | 6.12 | — |
| 694 (1) | 6.12 | 6.8 | 6.9 | 6.13 |
| 694 (2) | 8.27 | 8.30 | 8.30 | — |
| 694 (3) | — | 8.29 | 8.33 | 8.31 |
| 694 (4) | — | 8.13 | 8.9 | 8.7 |

In the case of cocksfoot, as of so many other species, it happens that the late strains tend to be multi-tillered and long lived. It would follow therefore from what has been previously stated that the early strains can only occupy habitats in quantity where inter-pollination leading to abundant seed setting accompanied by suitable conditions for seedling establishment, and followed by restricted grazing, are to be met with—that is to say, not on dense swards: for since these plants are not intrinsically long lived, new crops must be continually forthcoming if anything approaching habitat domination is to be assured.

It is very significant that not only on old swards where inter-pollination is necessarily restricted, but also on cliff habitats where the conditions are not favourable to establishment and early growth, it is the later and denser and more perennial types of cocksfoot rather than the early and shorter lived that alone maintain a firm footing.

The early and late strains are not compatible: it is always the dense and late which are favoured by excessive grazing, the early always suffering more from heavy defoliation than the late. The biotic factor—the control exercised

¹ See **Davies (2)**.

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by man and the effects of his grazing animals—is thus seen to have an overwhelming influence on ecotypical selection of cocksfoot, since it reacts decisively on the scope for free inter-pollination and upon the opportunities for the perennial strains to gain dominance. The early strains can only dominate partially or completely over the late if allowed to smother out the latter in the early stages of growth, and this the grazing animal will not allow.

The fact that cocksfoot maintains itself on very old swards is of considerable interest, and since the scope for inter-pollination is often very limited on such swards it is probable that re-establishment is due at least to some extent to seedlings that have been the result of selfing. The actual number of seedlings establishing themselves every year would presumably be very small, but since the vast majority of such seedlings would represent dense pasture and highly perennial types, a seedling once established would produce a plant capable of a very long life upon the sward.

The evidence would suggest that thickets perhaps afford the original and natural habitat for cocksfoot. Such habitats are more favourable than others to the greatest range of ecotypes; the growth is not so dense as to smother out the later and multi-tillered types in the early stages, while it is open enough to allow of sufficiently abundant seedling establishment to maintain the shorter lived early types.

From the point of view of the spread of this species, as indeed of the spread of any species, it is interesting to speculate as to the rival efficiency of the perennial habit accompanied by poor seed development and (or) of poor seedling establishment on the one hand, and of good seed development and (or) of good seedling establishment accompanied by plants of short duration on the other. On habitats where the perennial habit is of prime significance it is to be supposed that the introduction of a single plant or of a mere handful of individual plants—even of a normally cross-fertile species, provided a reasonable measure of self-fertility was also possible—might well be sufficient in the course of time to establish firmly a particular strain of the species so introduced. Thus, in connection with ecotypical selection and with the natural spread of a species, much may frequently have depended on the fact that reasonable self-fertility and self-vigour is often a possibility, even in a species like cocksfoot which is normally cross-fertile.

With reference to the gradual development of the old swards which now form so large a part of this country from other and pre-existing types of vegetation; and indeed with reference to the rapid spread of European species of grasses in parts of New Zealand and Australia, for example, even where these have never been intentionally sown, it is to be supposed that a certain establishment due to “selfed” seed would, in the early stages, have hastened the process enormously.

From the ecological point of view therefore, both in the widest sense and particularly in the segregation of ecotypes, it is perhaps as well to pay con-

siderable attention to the significance of the fact that a number of the cross-fertile species are also to a not inconsiderable extent self-fertile, and it is legitimate again to stress the fact that in nature indiscriminate hybridisation, even within the species, probably occurs far less than is usually tacitly assumed.

GENERAL CONCLUSIONS.

Except in cases where man has intentionally sown the seed in large amount, the introduction of a species in quantity into a new habitat must be a gradual process, and this is true in the main, even where the grazing animal passes from one type of vegetation to another, and may thus be a constant vehicle for the carriage of seed. In the present paper it has been shown that the species *Dactylis glomerata*, ecotypically considered, shows very marked habitat relationships—even when only broad habitat distinctions are brought under review.

It would seem to follow that conditions not sufficiently exacting to have reduced the representatives of a species to a single well-marked ecotype none the less operate to reduce the potential variability of the species as a whole within an inner circle of variability, and this despite the fact that new introductions from without must be to some, if only to a slight extent, continually taking place. The decisive effect of the sum of the habitat influences is not to be denied.

The investigations here reported are of profound interest in connection with the whole question of so-called acclimatisation, and show, of course, that it is impossible to form a correct picture of the attributes of any particular species unless and until truly representative individuals are collected from every characteristic habitat upon which the species occurs, and are brought together and grown under one set of uniform conditions.

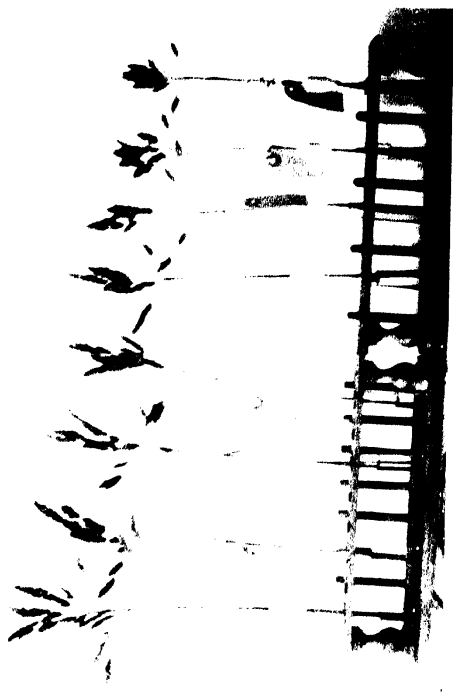
It is perhaps unfortunate that the work under review was necessarily conducted with restricted terms of reference—and economic terms of reference at that. Work of this sort can, however, only be conducted at a research station with very considerable outdoor facilities. At present it is only institutions working on economic terms of reference which have at their disposal the resources of such a station. It is to be hoped, however, that the time may not be far distant when Ecology in this country may be able to obtain sufficient financial backing to found for itself a station unhampered by agricultural or other economic calls upon its methods of enquiry. It is suggested that it is only by the study under uniform conditions of an enormous mass of carefully collected growing material representative of different species, accompanied by long continued breeding work, that it will be possible to elucidate with reasonable assurance the fundamental problems connected with the distribution, acclimatisation and evolution of plants.

ACKNOWLEDGMENTS.

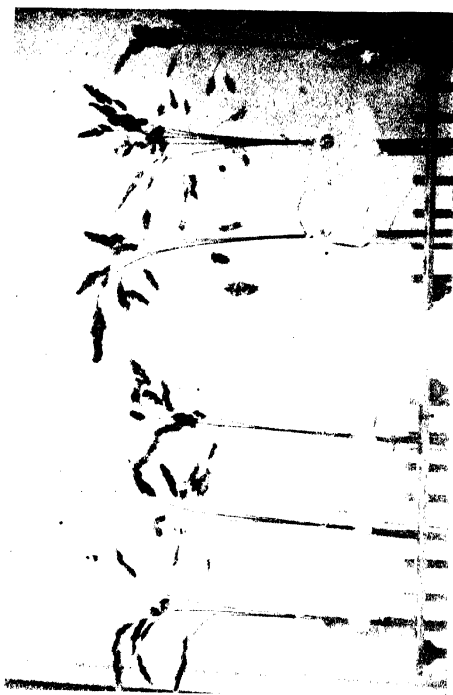
The writer desires to express his particular thanks to Dr J. G. Davies for permission to use the data on the panicle characters of cocksfoot and on the time of anther exertion, and also for much valuable assistance in connection with various measurements and records obtained during the more recent progress of the work. Thanks are also abundantly due to Mr A. R. Beddows and Mr W. E. J. Milton who have assisted in various phases of the investigation. The work would not have been possible without the accurate and careful assistance of Miss J. M. Le Mesurier (now Mrs H. Spring-Smyth) and Miss K. Grice, formerly assistants on the staff of the Station. Grateful acknowledgment is also made to Mr J. W. Watkins, Superintendent of Farm and Gardens, for his careful attention to all cultural details connected with the large number of seedlings and plants brought under review. The writer is indebted to Capt. Williams and to Mr D. Walter Davies for taking the various photographs. In conclusion, it is a pleasure to acknowledge the assistance of all those who helped in the collection of plants, in particular to Dr W. Brenchley of Rothamsted, Mr H. H. Dunn of Dunn's Farm Seeds, Salisbury, to Mr T. J. Jenkin, who was responsible for the Leicestershire collections, and to Mr Wm Davies, who made the Aylesbury collections.

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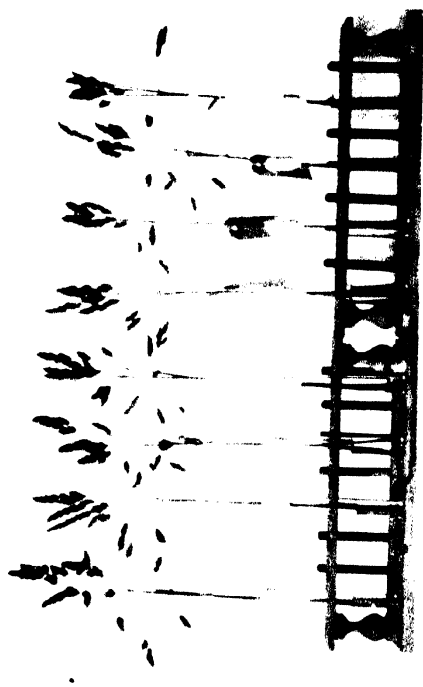
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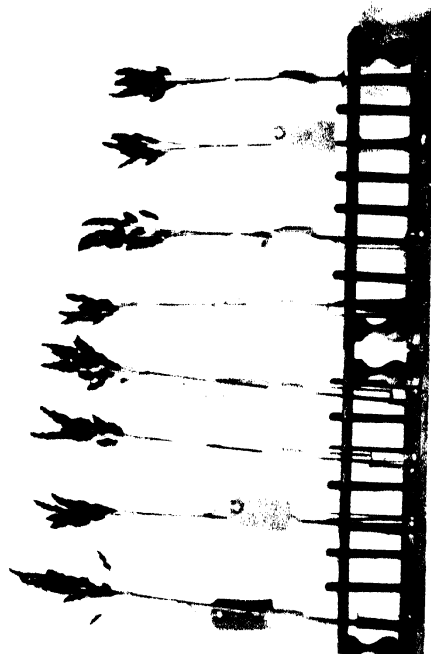
Phot. 2. Showing representative panicles of Class II:
erect; semi-compressed.



Phot. 4. Showing (on left) representative panicles of Class VIII:
drooping; semi-compressed; and (on right) representative panicles
of Class IV: semi-erect; spreading.



Phot. 1. Showing representative panicles of Class I:
erect; spreading.



Phot. 3. Showing representative panicles of Class III:
erect; compressed.

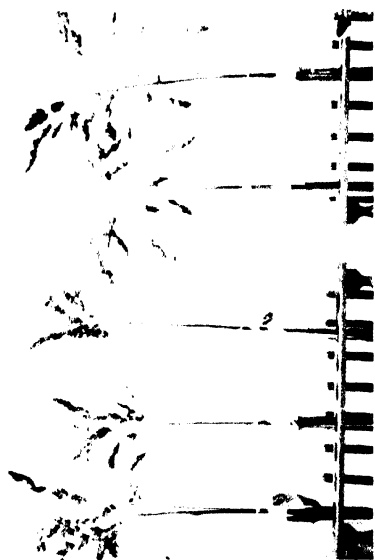
STAPLEDON--COCKSFOOT GRASS (*DACTYLIS GLOMERATA* L.):
ECOTYPES IN RELATION TO THE BIOTIC FACTOR



Phot. 6. Showing dense hay plants, indigenous and New Zealand
Photo, May 27th, 1927.



Phot. 8. Showing lax hay plants, Danish. Photo, May 27th, 1927.



Phot. 5. Showing on left, representative panicles of
Class V; semi-erect; semi-compressed; and on right
representative panicles of Class VI; drooping and
spreading.



Phot. 7. Showing dense hay plants, indigenous and New
Zealand: 1. inclined; 2. erect. Photo, May 21st, 1925.

STAPLEDON—COCKSFOOT GRASS (*Dactylis glomerata* L.):
ECOTYPES IN RELATION TO THE BIOTIC FACTOR



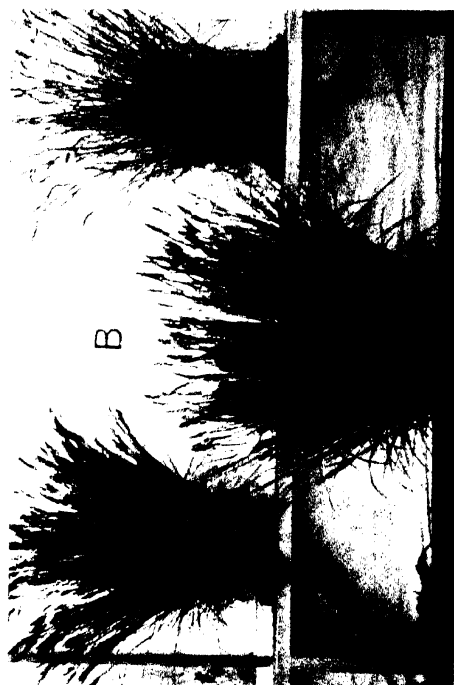
Phot. 9. Showing the most dense of the lax hay plants; Danish-b.
Photo, May 27th, 1927.



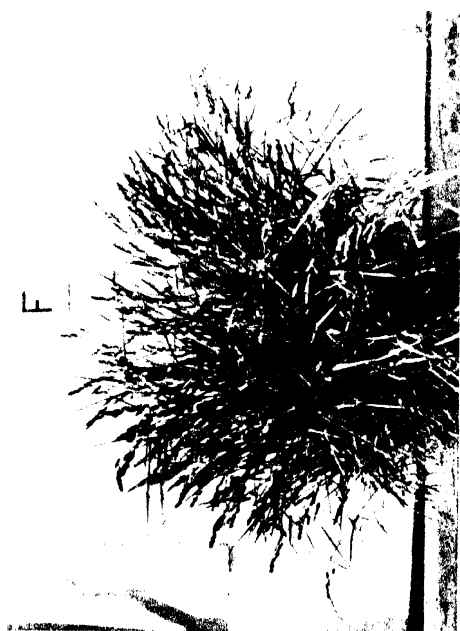
Phot. 11. Showing contrasting hay plants; above: 1, lax erect Danish; 2, dense inclined indigenous; below: 3, dense inclined indigenous. Photo, May 27th, 1927.



Phot. 10. Showing contrast between erect hay plant and dense cup. Photo, May 23th, 1925.



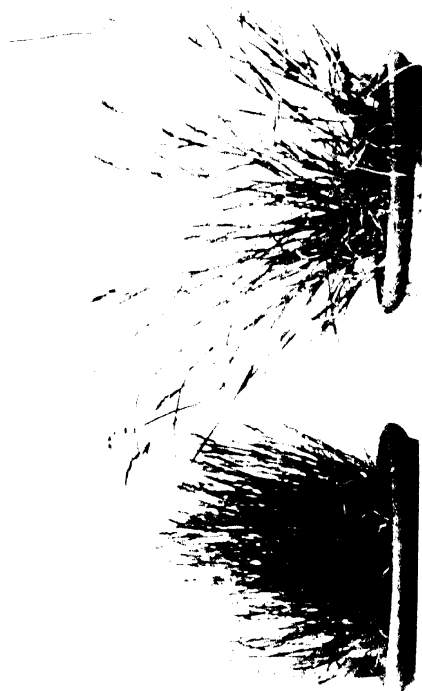
Phot. 12. Showing hay plants intermediate between lax hay and dense hay with excess of fine panicle-bearing tillers; indigenous. Photo, May 30th, 1927.



Phot. 14. Showing typical tussock. Photo, June 8th, 1927.



Phot. 16. Showing typical tussock. Photo, June 8th, 1927.

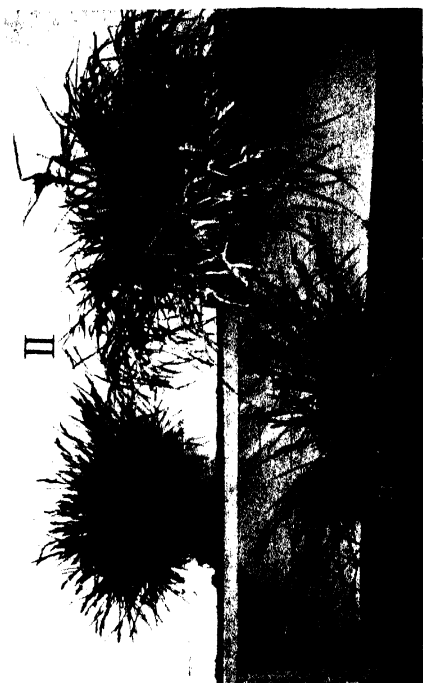


Phot. 13. Showing contrast between extra dense erect indigenous hay plant and less inclined Danish. Plants grown in sand. Photo, May 25th, 1926.



Phot. 15. Showing typical tussock. Photo, June 8th, 1927.

STAPLEDON—COCKSFOOT GRASS (*DICTYLIS GLOMERATA* L.):
ECOTYPES IN RELATION TO THE BIOTIC FACTOR



Phot. 18. Showing less desirable types from Leicestershire collections: *above*: 1. early dense pasture; 2. medium early crop; *below*: early crop. Photo, May 27th, 1927.



Phot. 20. Showing pasture types from Leicestershire collections: 1. spreading pasture; 2. dense pasture, very fine leaved; 3. spreading pasture. Photo, May 21st, 1925.

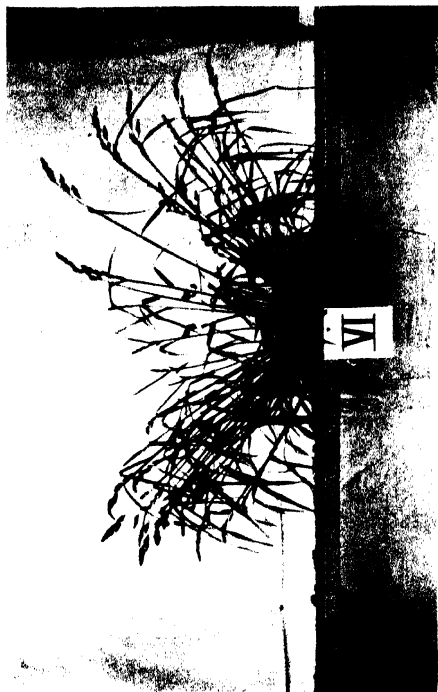


Phot. 17. Showing best and late pasture types from Leicestershire collections: *above*: 1. and 2. dense pasture; 3. spreading pasture; *below*: 1. dense pasture; 2. spreading pasture. Photo, May 27th, 1927.



Phot. 19. Showing pasture types: *above*: 1. dense pasture; 2. spreading pasture; 3. dense pasture; 4. dense pasture; *below*: 1. early dense pasture; 2. spreading pasture; 3. spreading pasture. Photo, May 30th, 1927.

STAPLEDON —COCKSFOOT GRASS (*DACTYLIS GLOMERATA* L.): ECOTYPES IN RELATION TO THE BIOTIC FACTOR



Phot. 22. Showing lax cup with very few barren tillers; Danish pasture, June 8th, 1927.



Phot. 24. Showing pasture plants with very few panicles: 1. dense pasture; 2. dense pasture; 3. spreading pasture. Photo, June 8th, 1927.



Phot. 21. Showing aloof; 1. tussock-dense pasture; 2. small dense cup. Photo, May 27th, 1927.



Phot. 23. Showing intermediate cup with considerable development of barren tillers; New Zealand. Photo, June 8th, 1927.

STAPLEDON—COCKSFOOT GRASS (*Dactylis glomerata* L.):
ECOTYPES IN RELATION TO THE BIOTIC FACTOR

ON THE DISTRIBUTION OF FRESHWATER TURBEL- LARIA IN THE ABERYSTWYTH DISTRICT, WITH ESPECIAL REFERENCE TO TWO ICE-AGE RELICTS

By KATHLEEN E. CARPENTER.

(With three Diagrams and three Maps.)

IN the course of a general survey of the freshwater fauna of the Aberystwyth district (1), the occurrence of the following species of Turbellaria-Tricladida was recorded:

Dendrocoelum lacteum (Muller).
Polycelis nigra Ehrenb.
Planaria albissima Vejd.

Planaria alpina (Dana).
Polycelis cornuta (Johnson).

The two first mentioned require but little comment: both are common in Britain (2), and in this district they are found in their characteristic situations, *Polycelis nigra* very generally in ponds and near the margins of muddy streams and backwaters, and *Dendrocoelum lacteum* in weed-grown streams: the latter species is rather rare in this district, and its place appears to be taken to a certain extent by *Planaria albissima*. The occurrence of this last-named species is of peculiar interest, as it has so far been recorded from no other British area, and from very few on the European continent (3, 4, 5). Reference has been made elsewhere (26, 27) to its very general distribution in streams of the Aberystwyth area: there is in fact no stream in which I have failed to find it, although it may be absent from some of the slow moving, boggy reaches of the high moorland brooks, but even in these it occurs wherever a small patch of stones provides the necessary shelter. It is on the whole most abundant in backwaters and relatively muddy reaches, and in springs of the limnocene type. Transverse fission is common, especially in early summer: the "buds" are at first without eyes or definite head. Sexual reproduction appears to occur during most of the year, but I have failed to find mature specimens between July and September. Although there is as yet no certain record of the occurrence of this species elsewhere in Britain, Whitehead (26) has found near Leeds immature individuals which most probably belong to it, and the extreme frequency round about Aberystwyth, as well as the tolerance of widely varying conditions, make it seem highly probable that it might be found, if sought, in other British areas. I have myself had specimens from the Llyfnant Valley, in the extreme North of Cardiganshire.

The two remaining species, *Planaria alpina* and *Polycelis cornuta*, have been recorded from a very few areas in Britain (21), but no systematic work has been done in this country on their distribution, although it presents features of a very high degree of interest, and has been the subject of detailed

investigation on the part of a number of Continental workers. On the European mainland *Planaria alpina* has a very wide, but sporadic distribution, occurring typically in Alpine and Scandinavian glacier brooks and in spring brooks of consistently low temperature in highland areas: it has also been found in high Alpine lakes (5). Kennel (4), from his observations on distribution, suggested that the species was a relict of the Great Ice Age, at one time general over Central Europe, but now surviving only in the cooler streams, and this theory has received confirmation in the shape of a large number of records from the cold stenothermal waters of the head regions of mountain brooks in a great variety of districts of Central and North-Western Europe, as well as through more detailed investigations of special areas. Voigt's extended researches (6, 9, 10, 13, etc.) led him to associate with *Pl. alpina* two other Triclad species, *Polycelis cornuta* and *Planaria gonocephala*, both of which are also common in mountain brooks, where *alpina* usually occupies the highest reach below the spring, and *cornuta* the middle zone, which slightly overlaps those of *alpina* above and *gonocephala* below. Although all three species are not invariably present in the same brook, the order of succession and the association of *alpina* with constant low water temperatures, of *cornuta* with temperatures slightly more variable but still narrow in range, and of *gonocephala* with the very much more variable temperatures which prevail in the more open courses of the lower brooks, are very regular. Accidental distribution, e.g. by water birds, is not likely to be frequent, as Voigt points out (13), since all three species usually hide under stones, and would also be liable to die from desiccation in transport, nor are their cocoons attached to objects likely to be carried in this way. The order of succession which prevails in so large a number of streams may therefore be considered to be a natural one, and referable to some general determining factor. On the known relationships Voigt based the theory that *Pl. alpina* was the earliest inhabitant of the streams during the Ice Age, and was forced to retreat towards the springs during the general climatic changes which ensued towards the end of this epoch, being replaced in the lower reaches by *Pol. cornuta*, which came in at a slightly later period, when the cold was less intense, and itself retreated before the incursion of *Pl. gonocephala*, a eurythermal type which probably appeared near, or even just after, the end of the glacial period. Voigt observed (10, 13) that, in the case of *alpina* and *cornuta*, unusually high temperatures inhibit vital activities to a certain extent, but on the whole he was of opinion that the limits of distribution of the three species were determined mainly by stress of competition between types similar in their feeding habits—a competition likely to be especially keen in cold mountain brooks where food (in the shape of insect larvae, etc.) is not very abundant.

Wilhelmi has questioned the status of *gonocephala* as an Ice-Age relict: he points out (22) that it is not necessarily a concurrent of the other two species, but occurs in many districts from which they are absent. He attaches far

greater importance than does Voigt to the direct action of changes of temperature in determining the limits of *alpina* and *cornuta*, and even suggests (12) that both species may wander from place to place, in accordance with seasonal changes, as in winter the temperature of the springs is often higher than that of the brooks below—a suggestion to which an isolated observation made by Führmann (7) seems to lend colour.

A somewhat new conception was introduced by Steinmann (14, 15), on the grounds of detailed observations made in the Jura, Schwarzwald, Alps, and on the Karst, which emphasises in particular the effects of variations in temperature on the physiology of reproduction in the species concerned. He points out that in the high Alps *alpina*, according to Zschokke (5), reproduces sexually throughout the year, but in lower regions it does so only during the winter season, the "sexual temperature" being about 5°–6° C. (Zschokke's finding of *alpina* mature at 10° C. at Lorenzbad he regards as highly exceptional.) He also notes that in *alpina* asexual reproduction is not a normal occurrence, as it is in *gonocephala* and some other species, where eyes and pharynx develop before the bud is released, but an incomplete and hurried process, readily induced by sudden changes in temperature, and exposing the new individuals to grave danger during the early phases of separate existence. Asexual multiplication of this type is likely to weaken the race, which is also weakened by being denied the power of sexual reproduction during a part of the year. Steinmann notes also that *alpina* occupies, not so much the coldest portions of the brooks, as those which enjoy the most constant temperatures, *gonocephala* those which have the widest range of temperature (*gonocephala* ranges as low as 0° C., and its "sexual temperature" is 13° to 17° C.), and *cornuta* the intermediate stretches: in other words, *alpina* is rigidly and very narrowly *stenothermal*, finding its optimum temperature at 5° to 6° C., and in winter occupying reaches which are actually warmer than those of *cornuta* and *gonocephala*. Steinmann suggests that the distribution of the three species is directly dependent upon the range of variations in temperature as affecting the reproductive processes, although other factors, such as the degree of oxygenation of the water and the presence of lime-salts, may serve as contributory causes.

Thienemann's careful study of the distribution of the three species in the brooks of the Sauerland (19) has added much valuable detail to our knowledge of their relationships. Remarking that "in den verschiedenen Teilen eines Baches die chemischen und die biocoenotischen Verhältnisse diegleichen sind, und dass man daher als Erklärungsgrund für die räumliche Trennung der Wohnbezirke der einzelnen Strudelwurmarten *nur* die verschiedenen Temperaturverhältnisse in den verschiedenen Bachstrecken heranzuziehen braucht," Thienemann establishes the following figures as the result of an intensive study of the variations in temperature throughout the seasons in a number of brooks in the Sauerland:

The range of temperatures at which *Planaria alpina* occurs alone is 2.2° to 12.5° C.: it is found together with *Polycelis cornuta* at temperatures from 3.4° to 14.75° C., and together with *Pl. gonocephala* from 0.7° to 15° C.

Polycelis cornuta occurs alone from 0.5° to 15.75° C., and together with *Pl. gonocephala* from 1° to 15° C.

Pl. gonocephala occurs alone between 0.5° and 24° C.

Pl. alpina is frequently found sexually mature at temperatures between 7° and 10° C., but no higher: its lower limit of distribution appears to be very definitely determined by a maximum temperature of about 15° C., whether it occurs alone or in company with either *cornuta* or *gonocephala*.

The whole of Thienemann's observations serve to confirm Steinmann's view of the importance of *range* of temperature, acting through the reproductive function, in determining distribution.

Bornhauser (20), working in the neighbourhood of Basel, was able to show that, other conditions being equal, lime content of the waters has some influence over the distribution of species, *Pol. cornuta* being markedly absent from streams which have a high lime content, while *Pl. alpina* and *Pl. gonocephala* are particularly abundant there.

My own earlier observations in the Aberystwyth district, reported elsewhere (27), indicated the existence of some anomalies in the distribution of these glacial relicts, to which special attention has been given during the last twelve months. *Planaria alpina* and *Polycelis cornuta* are both found in a number of streams in the district, but *Pl. gonocephala* appears to be entirely absent, a circumstance which may be related to the scarcity of lime-salts (see below, p. 111), and possibly to the extraordinary abundance of *Pl. albissima*, which is in possession of all the reaches in which *gonocephala* might be expected to occur.

The occurrence and relations of *Pl. alpina* and *Pol. cornuta* are, broadly speaking, in fair agreement with those observed on the Continent, but there are interesting variations for whose elucidation some little explanation of local topography is necessary.

The area surveyed in detail includes the whole valley of the Rheidol, a Cardiganshire stream, from its source on Plynlimon to the sea at Aberystwyth, a portion of the valley of the Ystwyth, which also rises in Plynlimon and debouches very near to the Rheidol, and that of the Clarach, a much shorter stream which joins the sea a mile or two north of Aberystwyth.

The area is extensively glaciated: its general character has been described by Keeping (2) as follows:

The whole country consists of monotonous repetitions of greywacke, hard shales and imperfect slates.... The whole country is mountainous: the hills are rounded and bare, and the highest ground is usually a dreary level waste of wet and boggy ground, dotted with lakes and pools. The two most important physical features of the district are two great plains of marine denudation which limit the height of the hills, truncating their tops, so that a view from the summit shows a great plain irregularly broken up by the river valleys. The lower plane rises gradually from 400-500 feet at the coast to 700 feet inland, and the higher plane starts abruptly at about 1100 or 1200 feet, and gradually slopes up to 1500 feet,

where it abuts against the highest island-like mass of Plynlimon... The Drift formations range over both these planes reaching up to within 100 feet of the highest ground. They consist principally of ice-formed stony clay or Till... In the interior of the country stony clays are of frequent and widespread occurrence in the valleys and along the sides of the hills, and they are particularly developed in the open parts of the valleys, where they form broad and thick sheets... In the Rheidol valley near Aberystwyth this drift was found to be 15 feet thick in a recent cutting, and it is probably much thicker in places.

Most of the streams draw their headwaters either from the peat bogs of the High Plateau or from marshy, sedge-grown tracts on the Low Plateau,

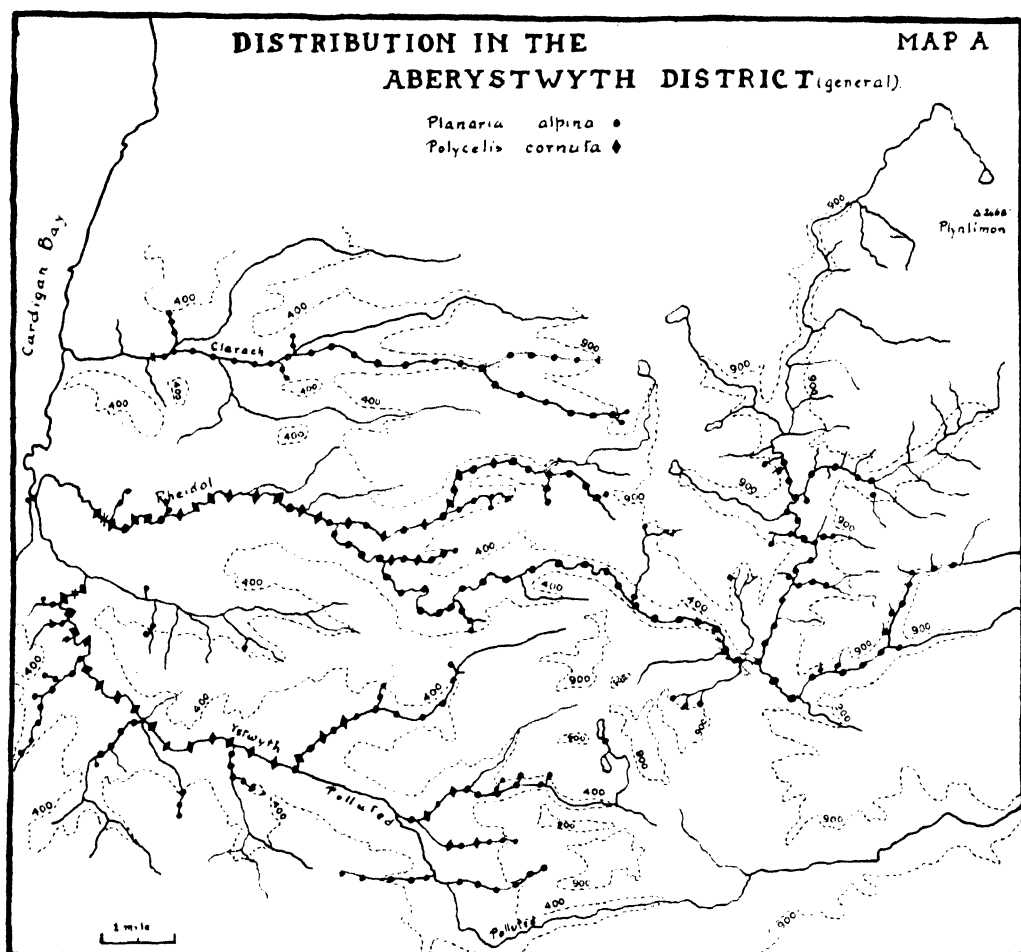


Fig. 1. Sketch map showing distribution of *Planaria alpina* and *Polyclis cornuta* in the Aberystwyth district.

and later in their courses receive increase from springs situated along the sides of the main trench-like valleys, often at the edge of the boulder clay. These springs are of two types:

(a) The true rheocrenes, opening into stony courses, whose water has usually pH 5.6-5.8 (probably owing to CO_2 dissolved under pressure: the pH 6.4-6.8 normal to the waters of most local streams is restored within a few yards of the spring), and dissolved oxygen content 80-100 per cent. of saturation values.

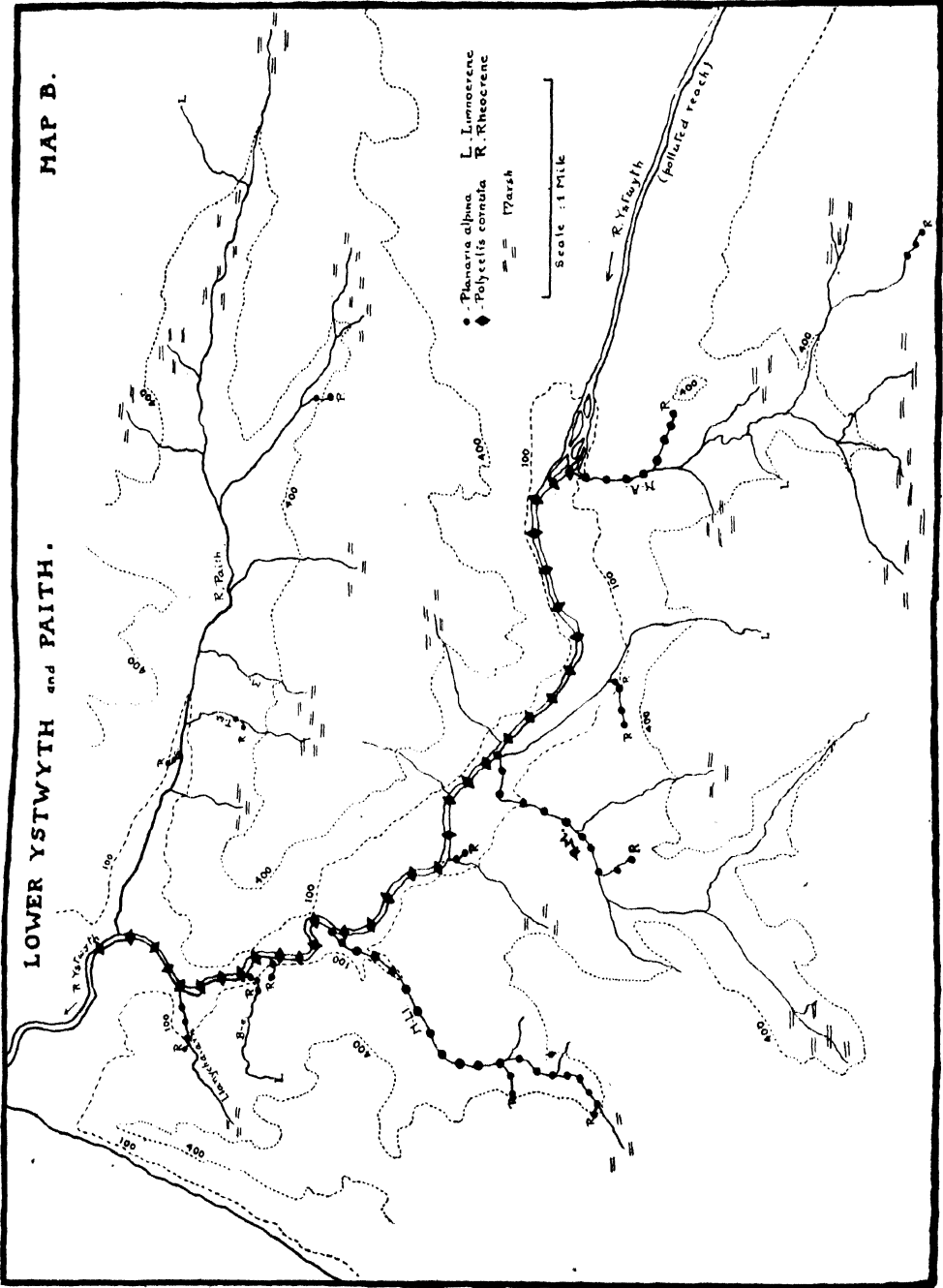


Fig. 2. Sketch map showing distribution of *Planaria alpina* and *Polycelis cornuta* in the river systems of the Lower Ystwyth and Faith.

(b) The limnocrenes, occurring on the boulder clay or in the marshy hollows, which receive a good deal of seepage water, have pH usually about 6.6, and pass into streams predominantly muddy in type, yet with a good many scattered stones.

The distribution of *Planaria alpina* (see Fig. 1) is largely dependent on the occurrence of rheocene springs: it has nowhere been found at a height greater than 1000 feet, and is entirely absent from the Upper Rheidol waters in the high peat-bog area; it is, however, found in a large number of tributary streams rising both on the edge of the High Plateau and at lower levels, and occurs in the Rheidol itself from the head of the gorge at Pont Erwyd down to Capel Bangor, a point five miles from the coast and only 100 feet above sea-level; a few specimens have been taken in the Rheidol only one mile from the sea, but these were probably "strays" from a communicating spring brook. In the Ystwyth valley, *alpina* is abundant in spring brook tributaries: a few captures (again, probably "strays") have been made in the Ystwyth below Llanilar (five miles from the sea), but above this point the main river is so seriously affected by pollution from lead and zinc workings that no satisfactory survey can be made. In the Clarach, *alpina* occurs along the whole length of the main stream and in several rheocene tributaries, and the range actually extends down to Llangorwen Bridge, a mile from the sea and less than 50 feet above high-tide mark. Reference to Fig. 2 shows clearly the characteristic avoidance of marshy headwaters, and the appearance of *alpina* at rheocene springs, with extension down the main stream.

The range of *Polycelis cornuta* always follows upon and usually overlaps that of *Pl. alpina*; *cornuta* is very abundant indeed in many of the brooks, but I have never found it actually in any spring: limnocrenes are tenanted by *Pl. albissima* alone, rheocrenes by *Pl. alpina* (occasionally with *albissima*),

Lime content of 26 streams in the Aberystwyth district.

| A High Plateau | | | B Low Plateau and plain sections | | |
|---------------------------------|----------------------------|-------------|-------------------------------------|----------------------------|----------------|
| Stream (reference number) | CaO (mgr. per litre) | Species | Stream (reference number) | CaO (mgr. per litre) | Species |
| 1 | 1.26 | <i>l</i> | 11 | 2.24 | <i>l</i> |
| 2 | 0.70 | <i>a, l</i> | 12 | 1.96 | <i>a, l</i> |
| 3 | 1.26 | <i>a, l</i> | 13 | 1.96 | <i>a, l</i> |
| 4 | 0.98 | <i>l</i> | 14 | 1.12 | <i>l</i> |
| 5 | 2.52 | <i>a, l</i> | 15 | 0.98 | <i>l</i> |
| 6 | 1.12 | <i>a, l</i> | 16 | 1.96 | <i>a, l</i> |
| 7 | 1.12 | <i>l</i> | 17 | 2.52 | <i>a, l</i> |
| 8 | 0.42 | <i>l</i> | 18 | 2.10 | <i>a, c, l</i> |
| 9 | 0.70 | <i>l</i> | 19 | 1.12 | <i>a</i> |
| 10 | 0.70 | <i>l</i> | 20 | 1.12 | <i>a, l</i> |
| | | | 21 | 0.98 | <i>a, c, l</i> |
| | | | 22 | 1.96 | <i>a, l</i> |
| | | | 23 | 1.82 | <i>a, l</i> |
| | | | 24 | 2.52 | <i>a, l</i> |
| | | | 25 | 1.26 | <i>a, c, l</i> |
| | | | 26 | 2.10 | <i>a, c, l</i> |

even when they occur at very few feet below sea level. *Polycelis cornuta* never occurs at a height of more than 900 feet, and its range extends down to the limit of tidal influence (about one mile from the sea) in Rheidol and Ystwyth: it is altogether absent from the Clarach.

The lime content of 26 samples from streams of the district is given above, with symbols *a*, *c*, *l*, indicating the presence of *Pl. alpina*, *Pol. cornuta* and *Pl. albissima* respectively. The figures, consistently low, are of interest in connection with Bornhauser's conclusion (see above, p. 108) that a low lime

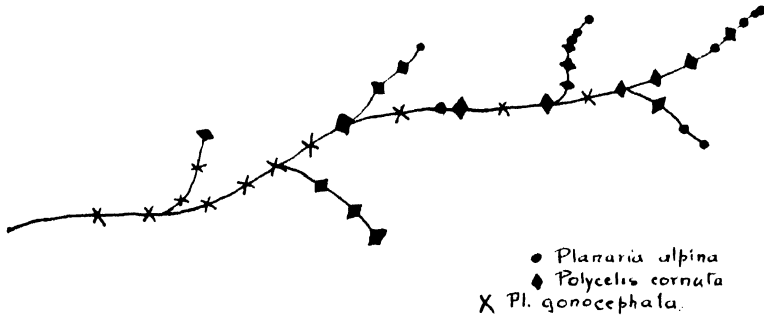


Fig. 3. Typical distribution of Planarian Ice-Age relicts in European mountain-brooks. [Schematised—after Thienemann, Voigt, etc.]

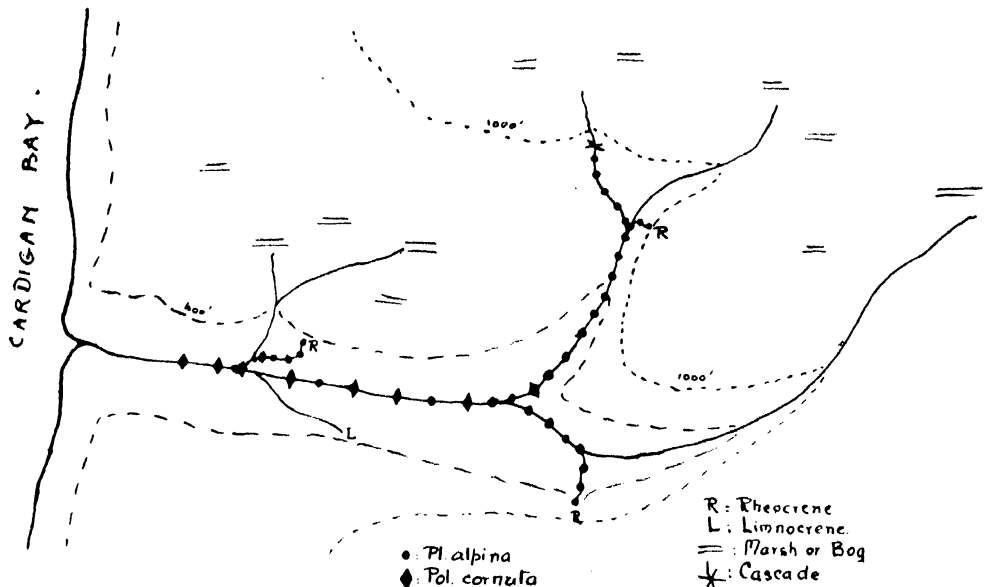


Fig. 4. Distribution of Planarian Ice-Age relicts in the Aberystwyth district. [Schematised.]

content is favourable to the presence of *cornuta*, the reverse condition to that of *alpina* and of *Pl. gonocephala*, a usual concurrent of the other two species which, however, does not occur at all in this district.

While the general Map A (Fig. 1) of distribution of the two relicts, *Pl. alpina* and *Pol. cornuta*, shows that their mutual relationships (always allowing for the complete absence of *Pl. gonocephala*, the usual third concurrent) are in

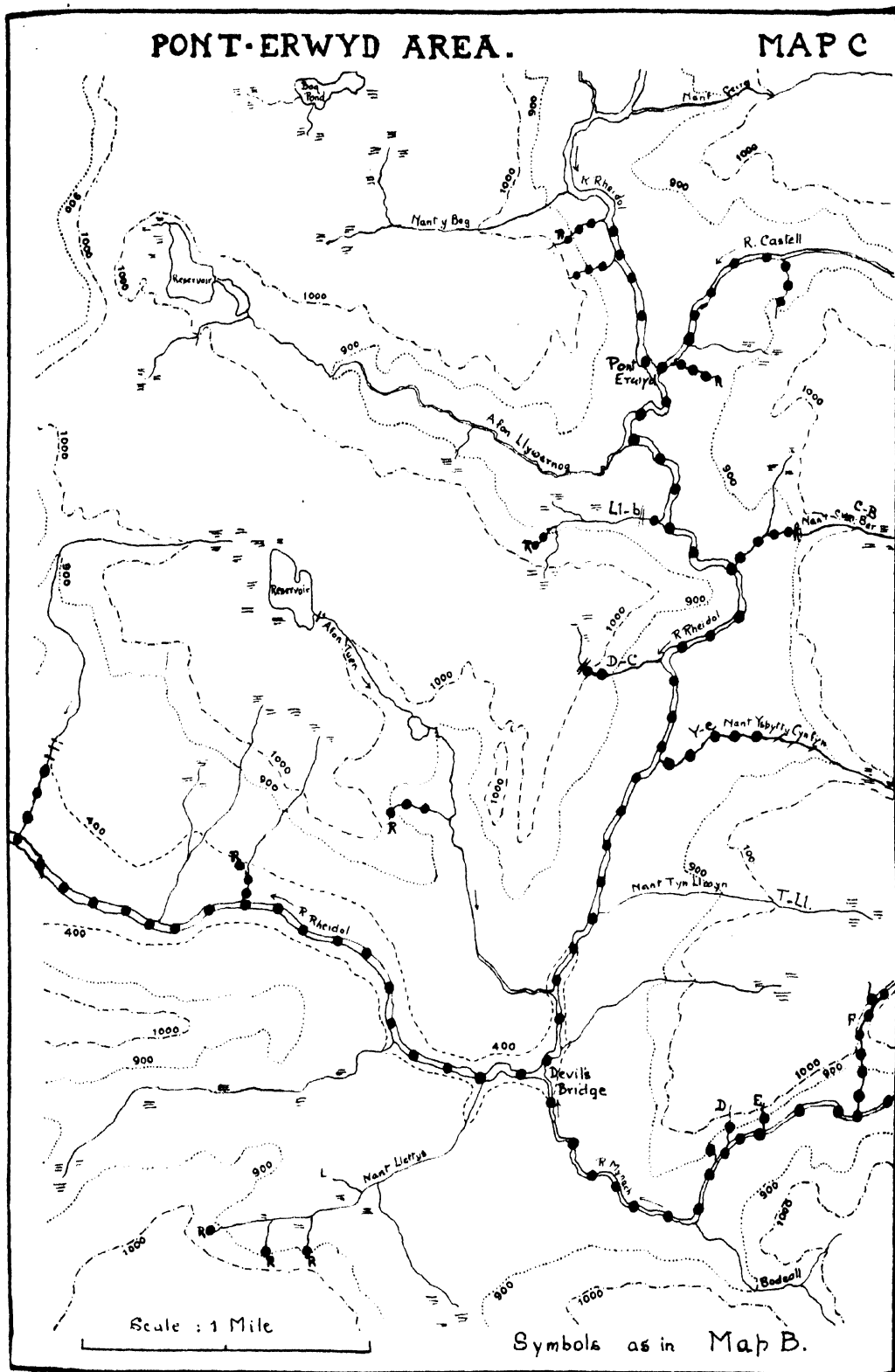


Fig. 5. Sketch map showing distribution of *Planaria alpina* in the Pont Erwyd and Devil's Bridge area.

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accordance with Continental discoveries, as illustrated by Fig. 3, some peculiar features remain to be explained. Apparently, in Continental areas, the range of all species is confined to really high ground: in the Sauerland, at latitudes 51° – $51^{\circ} 30'$ N. and altitudes 250–550 metres (i.e. 820–1804 feet), Thienemann (19) found *alpina* and *cornuta* only in the *higher* brooks of the whole series: in this area, latitude $52^{\circ} 30'$ – 53° N., I find the double range (see Fig. 4) extending between altitudes 50 and 1000 feet above sea level: it would appear, in fact, that both zones have been shifted several hundred feet downward from their normal position. Two problems present themselves for solution:

(1) Is the local distribution of the two species, apparently anomalous in its extension to low altitudes, in accordance with their stenothermous character as established on the Continent?

(2) What factor or factors can account for the absence of *Pl. alpina* from moorland brooks of high altitude and for its sudden appearance in lower reaches of these same brooks without the intervention of rheocene springs? (This highly peculiar feature is illustrated in Map C, Fig. 5, where *alpina* appears in the lower reaches of brooks Ll—b, C—B, Y—C, D—C, E, F and G—initials are substituted for the cumbersome local names—although there are no springs above its zone.)

For the solution of the former problem and, in part for that of the latter also, a careful record of seasonal variations in temperature of the waters was necessary. Three representative areas were selected for intensive study, and each was visited at least once a fortnight throughout a period of 12 months (June 1926–27): the results will be reported separately.

I. THE LOWER PAITH AREA (included in Map B, Fig. 2).

In this lowland district, the Paith, rising in marshy ground, flows over a valley carpeted with boulder clay to its confluence with the Ystwyth. *Pl. albissima* occurs in the Paith and all its tributaries, *alpina* in only three rheocene tributaries, and *Pol. cornuta* not at all. The results of a series of temperature records from the Paith (P), from one limnocene tributary (M), and from the two rheocenes (S and T—w) may be condensed as follows:

| Annual range of temperatures | | | | | | |
|------------------------------|--------------|--------------------|--------------------|------------|---------------|------------------------------------|
| Stream | Date | Max. temp. ° C. | Min. temp. ° C. | Date | Range ° C. | Occurrence of <i>Pl. alpina</i> |
| P | 14. viii. 26 | 19.5 | 2 | 12. ii. 27 | 17.5 | — |
| M | " | 22 | 2.5 | " | 19.5 | — |
| S | " | 16 | 6 | " | 10 | + |
| T—w | 16 ix. 26 | 14.5 | 6 | " | 8.5 | + |

Here, the occurrence of *alpina* appears to be typical: it is confined to the few relatively stenothermal waters and avoids those reaches in which temperature varies over a wide range, although the maximum temperature at which it has been found is just a point above Thienemann's maximal figure (18)

of 15° C. Sexually mature specimens were found in S and T—w only between 6° and 10° C. (January to May, 1927): this also is in accordance with Continental records.

The absence of *Pol. cornuta* from the Paith, as also from the Lower Clarach, in spite of the apparent suitability of the thermal range, I attribute to the large amount of boulder clay present in the valleys of these two streams.

II. THE LLANYCHAIARN AREA (included in Map B, Fig. 2).

In this second lowland district, the Llanychaiarn brook, rising in a marshy hollow about a mile above its junction with the Ystwyth, receives a large rheocrene spring about midway in its length. *Pl. alpina* is present at all seasons in vast numbers under the stones just below the spring and in a small rocky gully which ensues, and occurs sparsely in the lower part of the brook, which has an open course through meadowland: I have never found it either in the upper reaches of the brook or in the Ystwyth below the confluence. *Pol. cornuta* occurs in the Ystwyth, but not in the brook. *Pl. albissima* is everywhere abundant, especially above the spring. The temperature range during 12 months was as follows:

| Annual range of temperatures | | | | | |
|------------------------------|--------------|--------------------|--------------------|------------|---------------|
| Locality | Date | Max. temp. ° C. | Min. temp. ° C. | Date | Range ° C. |
| Upper section of brook | 30. vii. 26 | 22.5 | 2.5 | 1. xii. 26 | 20 |
| Spring section | 16. ix. 26 | 14.5 | 6.5 | 11. i. 27 | 8 |
| Lower reach of brook | 18. viii. 26 | 17.5 | 5 | 1. xii. 26 | 12.5 |
| R. Ystwyth | 18. viii. 26 | 20.5 | 5 | 1. xii. 26 | 15 |

The figures at face value give a somewhat wider range than the Continental standard: the maximum temperature in the brook (*alpina* range) exceeds Thienemann's limit by 2.5° C., and that of the Ystwyth is 4.3° C. above the same writer's maximum for *cornuta*, although in neither case is the minimum of 0.5° C. attained. Systematic collections, however, revealed the fact that the *alpina* and *cornuta* zones are by no means fixed: each has a summer and a winter range, the latter extending considerably below the former. In the case of *alpina*, although individuals are at all times numerous just below the spring, some specimens may always be found in the lower brook during the cooler months of the year, but between July 10th and September 16th, 1926, at temperatures of 14° C. and above, I was unable to find any at all in this reach, in spite of frequent and persistent search. An attempt to estimate the relation between numerical abundance and temperature was found to involve so many difficulties that I am obliged to content myself with a mere record of the fact that between July and September *all* the individuals were clustered at the spring, whereas throughout the remainder of the year *some* were always to be found along the whole course of the brook, these latter being invariably small individuals without fully developed sex-organs. I conclude that the real home and breeding-place of *alpina* is at the spring, but that

there is a certain tendency to spread downstream, only checked by the influence of high temperatures encountered in the lower reach in summer time. This view seems amply corroborated by laboratory experiments reported elsewhere (28), which have confirmed the possession by *alpina* of a strong negative rheotropism—a feature unusual in stream dwellers—which would undoubtedly encourage downstream migration, together with a marked sensitivity to changes in temperature leading to recoil from zones of thermal extremes. Evidence of a similar winter extension of the *alpina* range has been collected from several other brooks in the neighbourhood, but there are quite a number in which it does not take place: these latter (e.g. on Fig. 2, B—e, N—Ll, R—M and N—A) run the whole length of their courses in steep-sided and tree-shaded gullies, and the water temperature varies little from source to mouth (maximum summer temperature in N—A, a larger brook than the Llanychaiarn, just above its confluence with the Ystwyth: 15° C. only); in brooks of this special type the *alpina* range remains permanently extended to the confluence.

In the case of *Polycelis cornuta* there is undoubtedly a similar seasonal shift of some magnitude: I have found this species during the cooler months of the year in Lower Rheidol and Ystwyth down to the tidal limit (as mapped, A), but from the end of May to the beginning of September it is not to be found in the rivers below Capel Bangor (Rheidol) and Llanilar (Ystwyth), each five miles from the sea: at this season it is abundant in the tributary streams, and the maximum temperature at which I have actually collected it was 17° C. (Llanilar, May 10th, 1926)—only 1.25° C. above Thienemann's limit.

These observations appear fully to confirm Wilhelmi's conjecture (12) that *Pl. alpina* and *Pol. cornuta* may wander in the streams in accordance with the shifting of their zones of optimum temperatures.

The maximum temperature at which *alpina* was found sexually mature in this spring was 11.5° C. (June 19th, 1926), but I have a record of a single fully mature individual taken in a brook higher up the Ystwyth valley (Trawscoed, May 26th, 1926) at 13.5° C., a higher figure than any previously recorded.

The Llanychaiarn area was made the centre of observations on the relations between temperature variations and sexual maturity on the one hand, asexual multiplication by fission on the other, in pursuance of Steinmann's suggestions (14). About 100 individuals were collected at random on each visit to the spring, and the numbers of fully mature individuals and of those already notched preparatory to fission were noted: the results, expressed in percentages of the total number, are graphically rendered, together with the variations in temperature, in Fig. 6. It should be noted that in random collecting many of the smallest individuals are likely to be missed, so that most probably the recorded percentages both of mature individuals and of those in fission are higher than the actual; this error does not, however, seriously affect the relative significance of the curves, which distinctly evidence an inverse rela-

tionship between temperature and sexual maturity, a direct one between temperature and asexual fission. The additional records for summer 1927, after the completion of the original twelve-months' record, are inserted to illustrate the effect of the unusually cold weather which set in about the end of May in restoring *Pl. alpina* to what is really its winter condition (compare

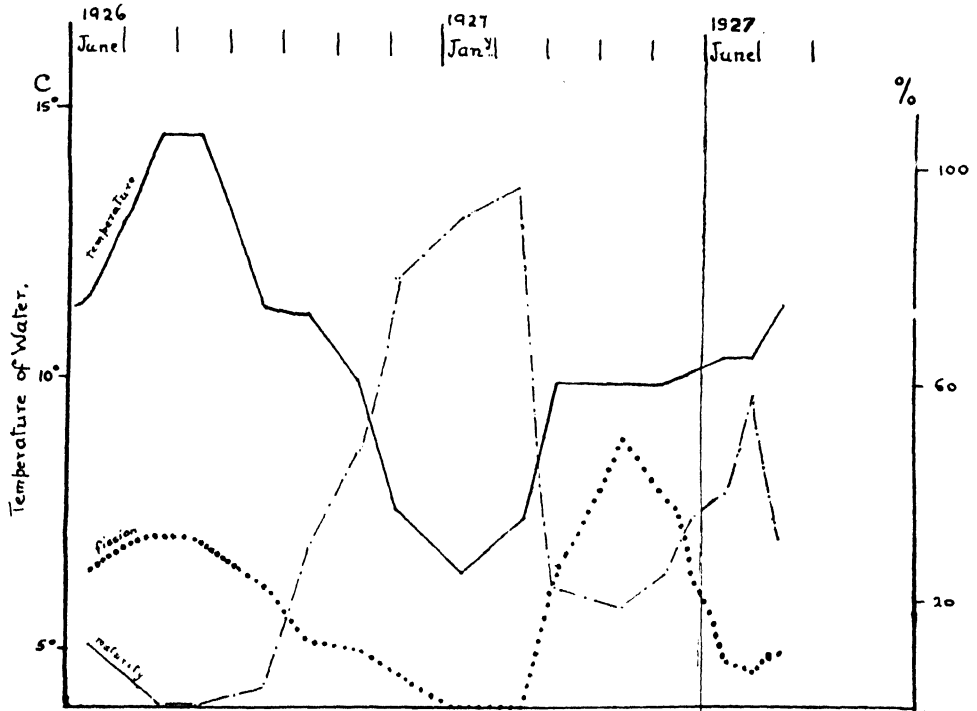


Fig. 6. *Planaria alpina*: sexual maturity and transverse fission in relation to temperature—Llanychaiarn spring.

June 1927 and November 1926), as well as the reverse effect of warmer weather in July. The form of the fission curve during the spring months may perhaps suggest that fission is dependent less upon absolute temperature than upon sudden changes, as Steinmann believes (14), but in this region of unstable climatic conditions it would be necessary to institute a very long series of close observations actually to prove the point.

Transverse fission, just behind the pharynx, is the rule in *alpina*; I have never seen it occurring in fully sexually mature individuals. I have observed in a number of specimens phases highly suggestive of the commencement of longitudinal fission, starting at one side between the head and the front end of the pharynx, but division of this type has not been observed by other workers, nor have I been able to follow the stages to complete fission. A forked appearance of the tail, corresponding to that which Steinmann observes in *Pl. teratophila* (18), is not uncommon, but does not appear to precede fission.

Pol. cornuta is active in transverse fission from April throughout the summer: the buds are heart-shaped, the new head growing from the notch. In the laboratory, the pharynx is formed usually two days after separation, and eyes begin to be developed after the eighth day: some degree of light sensitivity and a good deal of activity are, however, manifested by the fifth day of independent existence.

Comparison of the records obtained from the lowland (below 900') portion of the Aberystwyth district brings us to the following conclusions:

1. The characteristic *alpina-cornuta* sequence from the springs down stream is, on the whole, maintained.

2. The range of each species is surprisingly low in altitude.

3. The latter fact is partly explained by the relative stenothermy of waters even of the largest rivers in their lower courses, a feature probably ultimately due to the geologically recent subsidence of the old coastal plain of Cardigan-shire, which, by cutting off the true plain sections of the rivers, has exaggerated their average gradient and rate of flow.

4. Explanation is also afforded by the seasonal wanderings of both *alpina* and *cornuta*, which in winter extend their range much further down stream than in summer.

5. A further adaptation to changes in temperature consists in the loss of sexual maturity and frequency of transverse fission during the summer months.

III. THE PONT ERWYD AREA (Map C, Fig. 5).

From this plateau region, *Pol. cornuta* is entirely absent: *Pl. alpina* occurs in the under-mentioned reaches:

- (a) The R. Rheidol, which flows through a narrow and rocky gorge between Pont Erwyd and Devil's Bridge.

- (b) A few rheocene brooks (marked *R* on the map).

- (c) A portion of the Castell, a large tributary of the Rheidol.

- (d) The Mynach, a rather smaller stream.

- (e) The lower courses of a few brooks rising in peat bogs and later passing over cascades or long rapids (C—B, Y—C, D—C, Ll—B, B—d, and northern tributaries of the Mynach).

In each of these localities, I have collected *alpina* on the routine visits throughout the whole year: I therefore conclude that these reaches are within the *permanent* range of the species, and that this part of the range is unaffected by the seasonal migrations which extend or contract its lowland limits.

The obvious problem here is that of the avoidance by *alpina* of the upper moorland brooks, and of its sudden appearance in their lower reaches, without the intervention of true springs.

Temperature records for 1926–27 were as follows:

| Locality | Temperature range | | | | Occurrence of <i>alpina</i> |
|-------------------|-------------------|--------------------|--------------------|------------------|-----------------------------|
| | Date | Max. temp. ° C. | Min. temp. ° C. | Range ° C. | |
| Rheidol at Pont—E | 9. vii. 26 | 19.5 | 0.5 | 11. ii. 27 19 | + |
| Castell at Pont—E | " | 19 | 0.5 | " 18.5 | + |
| C—B above cascade | 17. ix. 26 | 18 | 2 | " 16 | — |
| C—B below cascade | " | 17 | 3 | " 14 | + |
| Y—c above rapids | " | 17 | 1.5 | " 15.5 | — |
| Y—c below rapids | " | 17.5 | 3 | " 14.5 | + |
| T—ll | " | 17 | 2 | " 15 | — |

A surprising feature is the high maximum for both Rheidol and Castell in July 1926: there is no possible doubt of the occurrence of *Pl. alpina* at these actual temperatures, since on each occasion the thermometer was inserted at the exact spot from which the specimens were taken. We are thus forced to the conclusion that *alpina* can, if necessary, endure for short periods a temperature of 19.5° C. in the streams—a conclusion which, though far overpassing the Continental field records, is in agreement with laboratory results, since I have been able to keep *alpina* alive and apparently unharmed in water whose temperature was raised in the course of three hours from 13° C. to 22° C., then allowed to fall gradually. Steinmann, however, reports (14) that even a gradual rise from 0° C. to 21° C. is fatal: one is tempted to conjecture that in this moorland area, where rheocrene springs are too scarce to provide adequate refuge from thermal extremes, the species may have acquired some degree of resistance to such extremes.

However that may be, it is obvious, by comparison, that the temperature range in the upper moorland brooks (C—B, etc.) cannot account for the absence of *alpina* from these reaches: the explanation must be sought in some character of the brooks themselves, and especially in the composition of their waters, since all the reaches in question lie below the zone of monotonous peat and *eaux sauvages* and have abundance of stony "beaches" for the Planarians to shelter—as *albissima* actually does.

Harnisch (25) has an interesting discussion of the causes of paucity of fauna in moorland waters: in the case of standing waters, he finds a wide range of temperature which may in itself be inimical to many species, but in the brooks (as exemplified above) the range is greatly narrowed. Other factors which may contribute to this paucity are (a) oxygen poverty in waters rich in decaying organic matter, (b) harmful action on the part of ferrous salts, which, according to Skadowsky (23), are abundant in some moor waters, and (c) efficacy of the "humic-acid" content itself. Harnisch finds that, although moorland water loses its efficacy on keeping, an imitation made by leaving pure soft water in contact with peat is fatal to certain invertebrate species, especially if the natural diurnal range of temperatures be also imitated. My own experiments with *Pl. alpina*, using fresh water from moorland brooks and also artificial peat water, show a very decided negative chemotactic reaction (28) induced by peat water of acidity pH 4.4 to 6.0: a similar reaction

is given by *Pol. cornuta*, but *Pl. albissima* (which is as common in moorland brooks of pH 5.6 and above as it is elsewhere, provided there are stones present) appears indifferent to peat water less acid than pH 5.0. All three species can survive three weeks' contact with peat water (containing a block of peat) when the temperature does not rise above 15° C. In another series of experiments, the temperature was gradually raised each day from 13° C. at 9 a.m. to 18° C. by 1 p.m., maintained at 18° C. for one hour, then allowed to fall gently, thus repeating a summer diurnal temperature cycle fairly well. About half the individuals of *alpina* so treated died after the first cycle, and all the remainder during the second; *Pl. albissima* seemed totally unaffected by the routine, and *Pl. alpina* in water from a lowland brook at pH 6.8 endured it for eight days, after which time the experiment was discontinued. (In this last experiment, of 10 *alpina*, all survived, but three underwent transverse fission, within the week—cf. p. 117.) The lethal action on *alpina* must then be due to a chemical reaction facilitated by changes in temperature: remains the question, what particular quality of the peat water is responsible for this reaction?

In a series of tests for the presence of iron in solution, only one sample from one of the reaches in question (C—B *a*) gave a positive result: the general action cannot therefore be referred to this factor.

Of the chemistry of "humic acids," little is known—not enough for a specific test which might definitely fix the responsibility (25).

Oxygen poverty may be, at any rate, partly responsible, as the following table shows relative poverty in the reaches devoid of *alpina*. The oxygen tests were made by the Winkler method, and the CaO percentages are also given in this table for reference, as Harnisch suggests (25) that the presence of lime salts in reasonable quantity may have some corrective influence on the biologically harmful character of moorland water.

[In view of a probable diurnal variation in oxygen values, similar to but on a smaller scale than the seasonal variation observed by Birge and Juday (*Wisc. Geol. Nat. Hist. Survey*, Bull. no. 22, 1911), the oxygen determinations were synchronised between 11.30 a.m. and 12.33 p.m.: the necessity for such a precaution has since been demonstrated by the records of actual diurnal variation published by Butcher, Pentelow and Woodley (*Biochem. Jour.* **21**, 4, 1927).]

| Locality | Oxygen content (expressed as % of saturation at the given temperature) | | CaO (mgr. per litre) | <i>alpina</i> |
|--------------|--|----------|----------------------------|---------------|
| | February test | May test | | |
| Castell | 94.3 | — | 0.70 | + |
| C—B <i>a</i> | 64 | 75 | 1.12 | — |
| C—B <i>b</i> | 86.4 | 99.8 | 2.52 | + |
| Y—c <i>a</i> | 76.9 | 68.4 | 0.84 | — |
| Y—c <i>b</i> | 93.3 | 92.3 | 1.12 | + |
| T—ll | 76.3 | 66.7 | 1.12 | — |
| Ll—b | 68 | — | 0.70 | — |
| S—b | 75 | — | 0.70 | — |

It may further be noted that *alpina* appears very sensitive to oxygen poverty in the laboratory: placed in a sealed vessel containing water impoverished by heating, it quickly dies; placed in a narrow tube filled with water and sealed at one end, *alpina*, if used in sufficient numbers, soon settles near the open end, regardless of the light stimulus; placed in shallow water containing decaying organic matter, *alpina* deserts its usual shelter under the pebbles provided for it, and crawls upon the surface film. In the experiment described on p. 120, in which *alpina* survived three weeks in peat water at medium temperatures, it was observed that, after a day or two, all the individuals came up to the surface film and for the most part remained there.

Whether oxygen poverty, "humic acid" content, or a combination of the two, be the responsible agent, no reasonable doubt remains that the upper moorland brooks are unsuitable for the tenancy of *alpina* in virtue of some characteristic of their waters, the effect of which is intensified by diurnal alternations in temperature: the sudden appearance of *alpina* at the foot of a cascade, as is very often the case, suggests very strongly that oxygen poverty alone is a serious matter.

SUMMARY.

The Turbellaria-Tricladide of the Aberystwyth area include three species whose occurrence is of peculiar interest: *Planaria albissima* Vejd., previously recorded only from Bohemia, but extremely abundant in this district, *Pl. alpina* (Dana) and *Polycelis cornuta* (Johnson), two species well-known on the Continent as Glacial Relicts, surviving on the high Alps and in cold stenothermous mountain waters in the Harz, Taunus, etc. Both species occur in Cardigan-shire streams almost down to the tidal limit, and neither has been found above the 1000-foot contour line. These apparent anomalies are explained with reference on the one hand to the geological history of the area, on the other to modifications in physiology and habit whereby the life cycle is adapted to the endurance of a temperate climate.

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Phot. 2. Nira Left Bank Canal showing gravelly substratum.



Phot. 4. Pravara Left Bank Canal, before clearing, showing the length cleared. The man is holding a bunch of *Potamogeton pectinatus*.



Phot. 1. Pravara Left Bank Canal showing patch of weeds on a convex bend.



Phot. 3. Vegetation on the floor of Mutha Right Bank Canal after draining and before clearing. The man is holding two bunches of the vegetation.

THE AQUATIC WEEDS IN DECCAN IRRIGATION CANALS

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(With Plate XVIII and six Figures in the Text.)

INTRODUCTION.

IN 1915 the Irrigation Department of the Bombay Presidency approached the Economic Botanist¹, Dr W. Burns, for advice regarding the serious blocking of irrigation canals by aquatic weeds. These weeds and the conditions of their growth have been studied intermittently from that date. The following is a short account of the results obtained. This paper does not aim at being a complete presentation of the problem nor is it a complete record of results. Various circumstances, particularly the difficulties of experiment on a canal scale, have prevented the work from being carried to its logical conclusion, but it is felt desirable to put on record what has been done, such as it is.

THE CANALS.

The Deccan canals were constructed with a view to bring into cultivation areas which have a precarious rainfall. These canals take their origin directly from large storage reservoirs in hilly tracts or pick-up weirs lower down. They are not to be compared in any way with the canals in the Punjab, either as regards length or volume. The three important canals dealt with are the Mutha Right Bank Canal, the Nira Left Bank Canal and the Pravara Left Bank Canal. The map (Fig. 1) indicates their position and extent.

The Mutha Right Bank Canal takes its origin from Lake Fife at Khadakvasla, about 11 miles from Poona. The total length of the Canal is 64 miles, of which the upper 13 miles have been studied for weed growth. This canal not only supplies irrigation for agriculture but also the drinking water supply of Poona City and is hence doubly important. It has a very tortuous course especially for the first 10 miles. The water, as a rule, is clear except during the monsoon. This is the most weedy of the three canals.

The Nira Left Bank Canal takes its origin from the Vir basin, which is 10 miles away from Nira station. This is the longest and the oldest of the canals. Its total length is about 100 miles, of which the upper 50 miles were examined

¹ My acknowledgments are due to Dr W. Burns for guidance during this work and for help in writing this article. (D.V.N.)

for weeds. It is the least weedy of all the canals and is peculiar in having only one species of weed. The water is usually silty.

The Pravara Left Bank Canal is a recent canal opened in 1919. It is exceedingly weedy. The total length of the canal is 44 miles and the length examined was the first 30 miles. The water is clear during the greater part of the year.

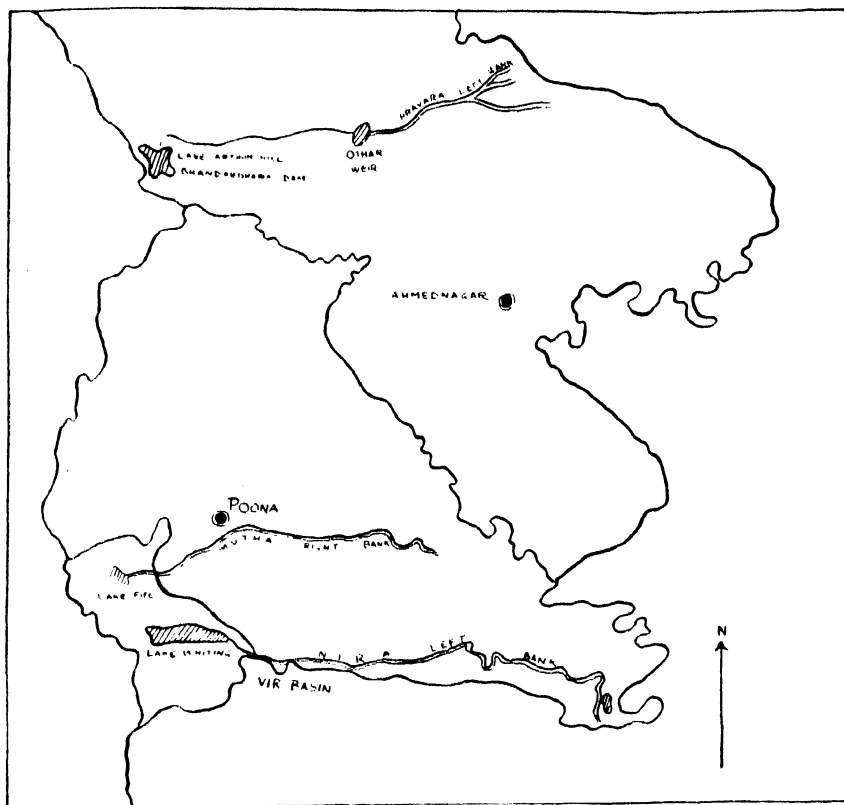


FIG. 1. Map showing the position and extent of the canals. Scale 40 miles to an inch. (Width of the canals exaggerated.)

THE NATURE AND AMOUNT OF BLOCKING BY WEEDS.

The problem presented was essentially a practical one. An idea of the blocking due to weeds can be got from the following statement by an irrigation officer:

“Even after a weed clearance, the discharge of the Mutha Right Bank Canal with 8 feet of water is only 320 cusecs as against 420 original designed discharge. And when full of weeds, which under some conditions takes place within two months, the discharge with the same depth falls to 95 cusecs, or less than 23 per cent. of the designed discharge.”

“In the case of the Pravara Left conditions are still worse, for whereas the canal when first opened in 1919 was capable of giving a discharge of 500

cusecs with only 6 feet of water, only 272 cusecs can be obtained now with that depth, and only 73 cusecs or 15 per cent. of the 1919 figure, after the weeds have grown, which occurred last year within $2\frac{1}{2}$ months of a full weed clearance."

It seemed necessary to determine first of all the species concerned and their distribution and then the conditions favouring them. It should be stated that these canals are cleared of weeds by hand during closures, some three or four times in the year. Unfortunately such closures cannot be extended for more than three or four days at a time. Hence the silt at the bottom never dries and many portions of rhizomes remain in the silt. The clearing cannot in any way be considered thorough.

THE WEED PLANTS.

The plants found are well-known aquatics and it is unnecessary to go, in greater detail, into their morphology, but some notes of their behaviour in these conditions may be not without interest.

Potamogeton perfoliatus L. This is the worst and the most widely distributed of the weeds. As mentioned by Arber (1), it produces leaves of a great variety of shape. The plant flowers in the Deccan in July and fruits in November. The fruits float for a time and then sink. We have been unable to get them to germinate in laboratory conditions. No perennating organs were observed. Reproduction seems to depend on the drifting down of natural cuttings and broken branches. These readily root when they come to rest. We have not observed deciduous winter shoots in this species. When piled on the bank, the weed material soon shrinks to a very small bulk and can be easily removed or burned.

Potamogeton indicus Roxb. This plant has two sets of leaves, aerial and submerged, with the usual internal difference between such kinds of leaves. The plant reproduces itself by suckers, natural cuttings and underground resting buds. The last are produced in conditions where there is a slow drying up of water, as in a pond. The flowers are formed in the month of December and the fruits in the month of May, in short compact spikes which stick out of the water. The fruits detach themselves and sink within 48 hours. We have not been able to observe germination in laboratory conditions. The plant is confined to the Mutha Canal.

Potamogeton pectinatus L. This plant, on account of its narrow leaves, does not obstruct the water quite so much as the two previous species. It reproduces itself by cuttings and underground tubers. The latter have been described by Arber (1). We were able to germinate these tubers in laboratory conditions. The plant flowers in September and fruits in February. We were not able to germinate the fruits.

Hydrilla verticillata Presl. reproduces itself by cuttings and tubers, underground and aerial. The underground tubers are produced on long whitish rhizomes which arise in the axils of the lower leaves. These lie buried in the

soil at a depth of 8 inches and germinate on the advent of the monsoon. The aerial buds are condensed greenish axillary shoots which are capable of becoming new plants when they fall in soil or water. Both these types of resting buds were observed in canal conditions. Flowering was not observed.

Vallisneria spiralis L. is a grass-like weed which has been many times described. Flowering takes place in March or April, but we have not found any fruits. The usual method of reproduction is by suckers. It is very hardy and is one of the pioneers of canal weed vegetation. It also exists in small distributaries where it is subject to drying up.

Ceratophyllum demersum L. This weed with clusters of divided leaves is not common. Sometimes in the apical regions of the shoot the leaves are crowded and deep green. This may be the winter growth described by Arber (1). The plant is anchored to the soil by rhizoid shoots. The usual methods of reproduction in the canals is by natural cuttings.

The following table shows the distribution of these species among the canals:

| Species | | | | Mutha Right Bank | Nira Left Bank | Pravara Left Bank |
|-------------------------|-----|-----|-----|---------------------|-------------------|----------------------|
| Potamogeton perfoliatus | ... | ... | ... | a. | absent | f. |
| P. indicus | ... | ... | ... | a. | " | absent |
| P. pectinatus | ... | ... | ... | o. | " | f. |
| Vallisneria spiralis | ... | ... | ... | a. | d. | f. |
| Hydrilla verticillata | ... | ... | ... | a. | absent | f. |
| Ceratophyllum demersum | ... | ... | ... | f. | absent | o. |

a. = abundant. d. = dominant. f. = frequent. o. = occasional.

ECOLOGY OF THE WEEDS.

When the canals were closed for cleaning, the writer took the opportunity of visiting them as often as possible. At such times the distribution of the weeds was much more apparent than when the canals were full. These observations led him to believe that weed growth was dependent on deposition of silt and that deposition of silt was dependent on the configuration of the canal and velocity of flow. Every convex curve had its own curved silt bed emphasising it (Phot. 1).

Wherever conditions led to the heading of water, silt was deposited. Thus, the sudden broadening of the section of the canal, obstacles such as over-bridges, stop-gates, etc., were all causes of silt deposit. The centre of the less affected canals where the velocity was greater than at the edges was practically free from silt. The Nira Canal, with a velocity of from 1.5 to 2.5 feet per second, deposits much less silt than the Mutha Canal with a velocity of 1.0 to 1.5 ft. per second. These observations correspond with those of Butcher (2) for the river Itchen.

While there is no question that deposited silt offers an admirable substratum for the growth of these aquatic weeds, it should be mentioned that there was, and is, a decided difference of opinion among irrigation engineers in the Bombay

Presidency as to the effect on weeds of silt *in suspension*. Certain engineers hold that suspended silt tends to eliminate the weeds by reduction of light. We have no critical experiments on this point. In any case, however, it is

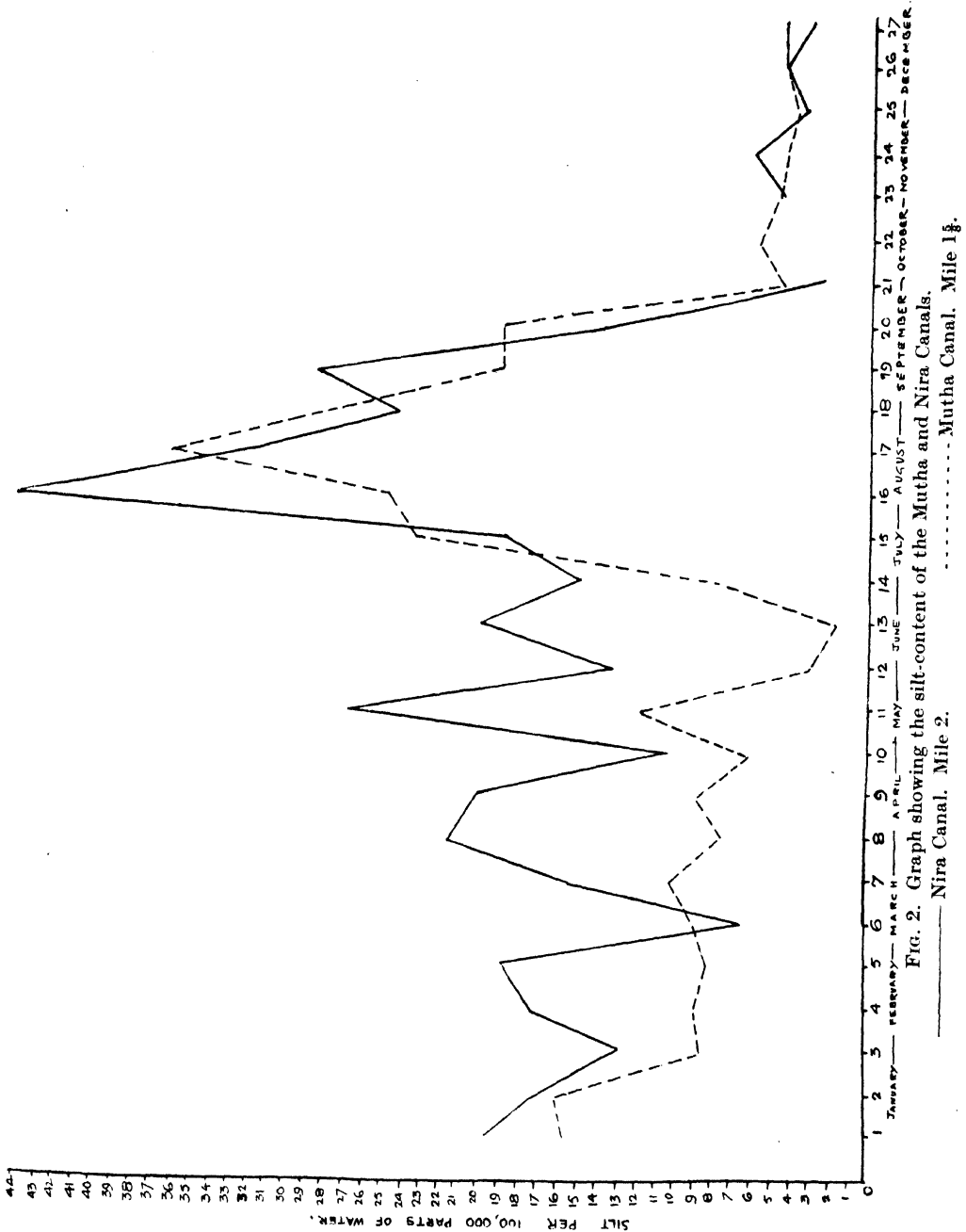
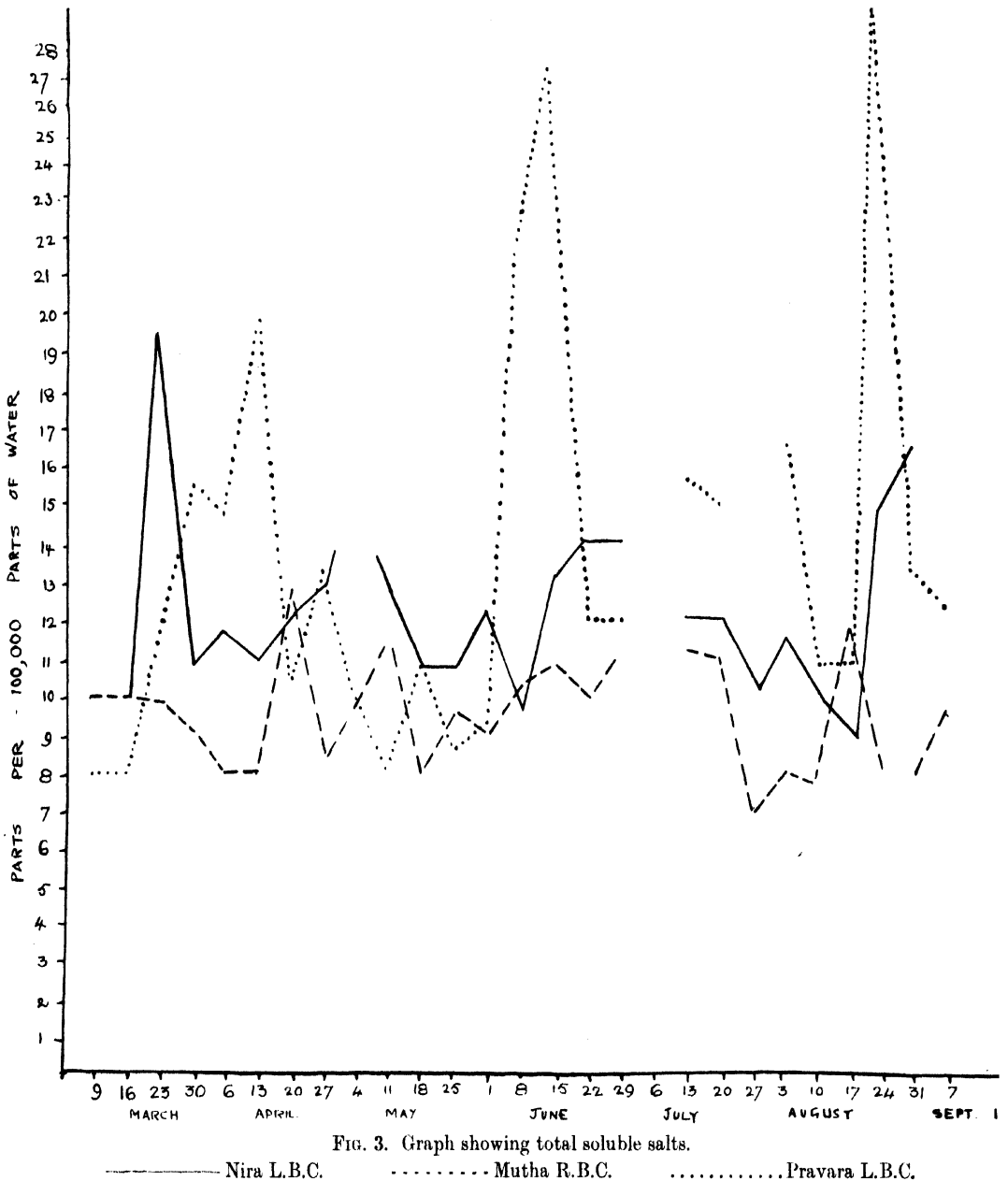


FIG. 2. Graph showing the silt-content of the Mutha and Nira Canals.

— Nira Canal. Mile 2.
 - - - - - Mutha Canal. Mile 1 1/2.

doubtful whether suspended silt would really affect the species of *Potamogeton*, the upper leaves of which at least are always just under the surface and get a great deal of light.

To get an accurate idea of the amount of suspended silt in two of these canals, we arranged to receive samples every week during the year 1922 from the Mutha Right Bank Canal at mile $1\frac{1}{2}$ and mile $8\frac{1}{4}$, and also from the Nira



Left Bank Canal at mile 2 and mile 8. These canals were chosen because the Mutha Right Bank Canal has usually clear water and the Nira Left Bank Canal has usually silty water. The graph (Fig. 2) indicates results. It will be seen that the Mutha Right Bank Canal carried decidedly less suspended

silt on the whole than the Nira Left Bank, although the difference is not so marked as we were*led to expect, nor is it absolutely uniform, there being occasions when the Nira Canal water contained less suspended silt than the Mutha. Two interesting facts are noticeable: (1) the great increase in suspended silt in both canals during the monsoon (June to October), and (2) the great decrease in suspended silt in the three months following (October, November and December). The last named three months are the months of maximum vegetative growth of the canal weeds.

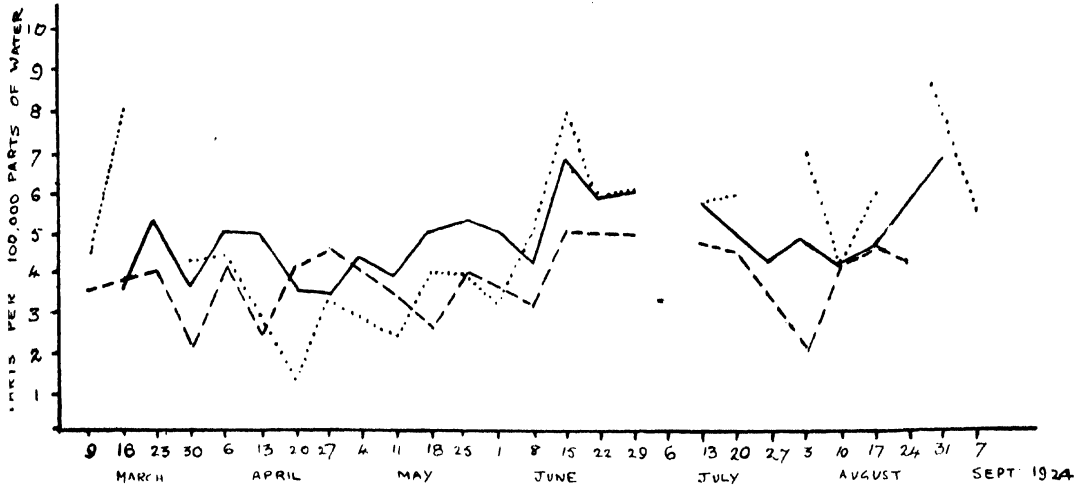


FIG. 4. Graph showing seasonal variation of calcium carbonate content of canal waters.

———— Nira L.B.C. - - - - - Mutha R.B.C. Pravara L.B.C.

CHEMICAL ANALYSIS OF THE WATER OF THE CANALS.

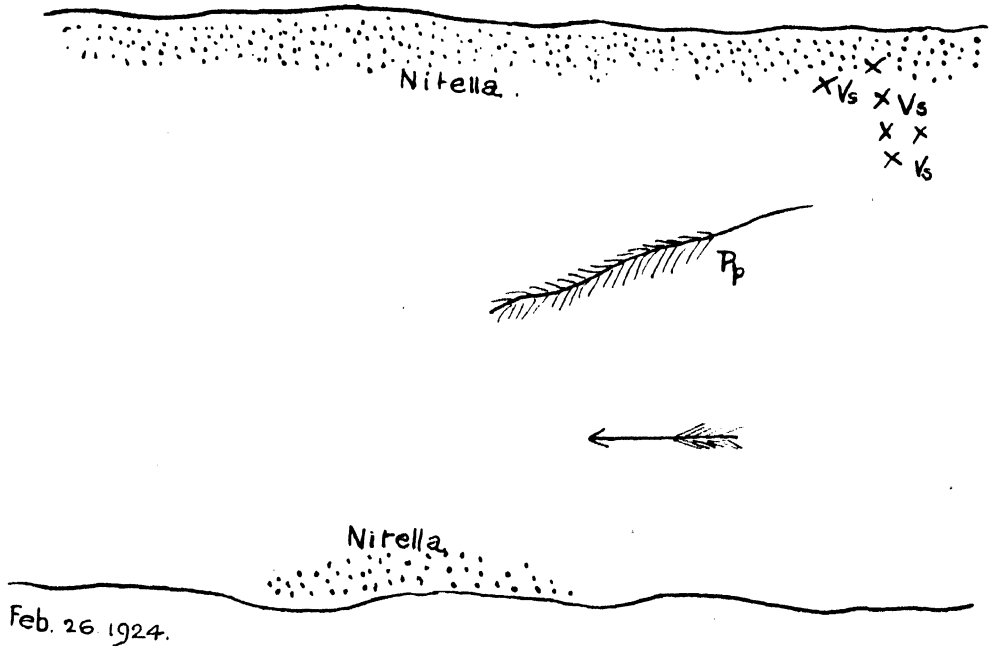
Samples collected on March 16, 1924, from the three canals gave on analysis the following results:

| Parts per 100,000 | | Nira Canal | Mutha Canal | Pravara Canal |
|---------------------|-----|------------|-------------|---------------|
| Total soluble salts | ... | 10.00 | 10.00 | 8.00 |
| *Calcium carbonate | ... | 3.50 | 3.50 | 4.40 |
| Magnesium carbonate | ... | 1.26 | 1.25 | 0.40 |
| Magnesium sulphate | ... | 0.75 | — | — |
| Magnesium chloride | ... | 1.90 | 0.62 | 0.30 |
| Sodium chloride | ... | 0.58 | 3.50 | 2.40 |

* Other calcium salts were absent.

Similar analyses were done weekly from March 9, 1924, to Sept. 8, 1924, and the two graphs show the fluctuations of (1) total salts, (2) calcium carbonate (Figs. 3 and 4). As regards total salts, there are considerable fluctuations both in the individual canals and in their relation to one other. The calcium carbonate graph is rather more consistent and shows the Nira Canal to be on the whole more chalk-bearing than the others. We cannot say that there is definite correlation between the species of weed present and suspended silt, total soluble salts or calcium carbonate.

Vallisneria spiralis, which is in the canal with the most silty water, does not seem to suffer from suspended silt. The non-appearance of the other species in the Nira Left Bank Canal is probably not due to the silt in suspension but to the lack of deposit of that silt. On account of the greater velocity of the canal, practically nothing is deposited in the first 10 miles, and the substratum is quite gravelly (Phot. 2). In the same canal lower down, at mile 48, weeds



Feb. 26 1924.
FIG. 5. Chart of a rocky section of the Mutha Right Bank Canal, showing vegetation on February 26, 1924.

XVs = *Vallisneria spiralis*.

Pp = *Potamogeton perfoliatus*.

were observed in patches, and it was found that wherever *Vallisneria* occurred, there was a bed of silt, 2 inches deep, beneath it. Absence of this species indicated a gravelly bed. As will be shown later, *Vallisneria* is a pioneer plant invading these canals.

The question of illumination naturally attracted the writer's attention to the allied question of depth at which these weeds can grow. The average depth of the above canal is about 10 feet. The various records of the depths in which the species mentioned can grow indicate that they will thrive at much greater depths.

At Madhmeshwar, the origin of the Godavari Right Bank Canal, *Potamogeton perfoliatus* was found growing in 20 feet of water. As has been already pointed out, *P. perfoliatus* and *Hydrilla verticillata* tend to produce their leaves in the top 2 feet of their length, and hence utilise all the light available. To get some experimental data on the effect of depth the writer carried out the following tests.

Two wooden tubs, *A* and *B*, each containing 9 inches of soil and six plants of *Potamogeton perfoliatus* of approximately equal vigour, were suspended in a well, *A* at a depth of 5 feet and *B* at a depth of 10 feet. This well was frequently disturbed by the leather bag with which water was raised, but there was no silt in the water. At first the tubs were taken up now and then to see the progress of the plants, but this was stopped as there was a tendency for the soil to be washed away during the lifting process. After a period of 144 days (March 7 to July 29, 1924) the total wet weight of the plants in tub *A* was 1300 grams, while that of the plants in tub *B* was only 24 grams. All the growth was removed by cutting the plants level with the surface of the soil and the tubs were again submerged, but their depths were now reversed, tub *B* now being at 5 feet and tub *A* at 10 feet. After 144 days (August 7 to December 28, 1924) tub *B* at 5 feet gave a growth of 687 grams, while tub *A* at 10 feet gave a growth of 618 grams.

When one considers the very small plants in tub *B* on account of its original submersion, it is fairly plain that 5 feet depth was much more favourable to the growth of the plants than 10 feet.

STUDY OF A DENUDED AREA ON THE CANAL BED.

In order to have some accurate idea regarding succession in these canals, we cleared a length of 39 feet of a rocky section of the Mutha Right Bank Canal at mile $5\frac{3}{4}$ during the closure in October 1923. Phot. 3 shows this length before clearing. The following weeds were present in abundance:

Potamogeton indicus.
Hydrilla verticillata.

Vallisneria spiralis.

This cleared area was not further touched and was revisited at succeeding closures. The following is a short description of the observations made:

On February 26, 1924, the whole area was covered with a very fine layer of silt. *Nitella* species had begun growing at the edges of the area. Detached plants of *Vallisneria* were found in one corner and a branch of *Potamogeton perfoliatus*, probably washed down from somewhere up the canal, was beginning to take root at the nodes. The accompanying diagram indicates the above graphically (Fig. 5).

On July 10, 1924, that is about eight months after the clearance, the layer of silt was an inch and a quarter deep. *Nitella* had made great progress and had occupied almost the whole area except a few places where rock was jutting through the silt. *Vallisneria* occurred throughout the area, all this invasion being the result of rhizomes penetrating the area from above. There were now two plants of *Potamogeton perfoliatus* and one plant of *Potamogeton indicus*. All apparently from natural cuttings.

On November 22, 1924, that is about 13 months after clearance, the silt was 2 inches deep. *Nitella* and *Vallisneria* had still further multiplied and

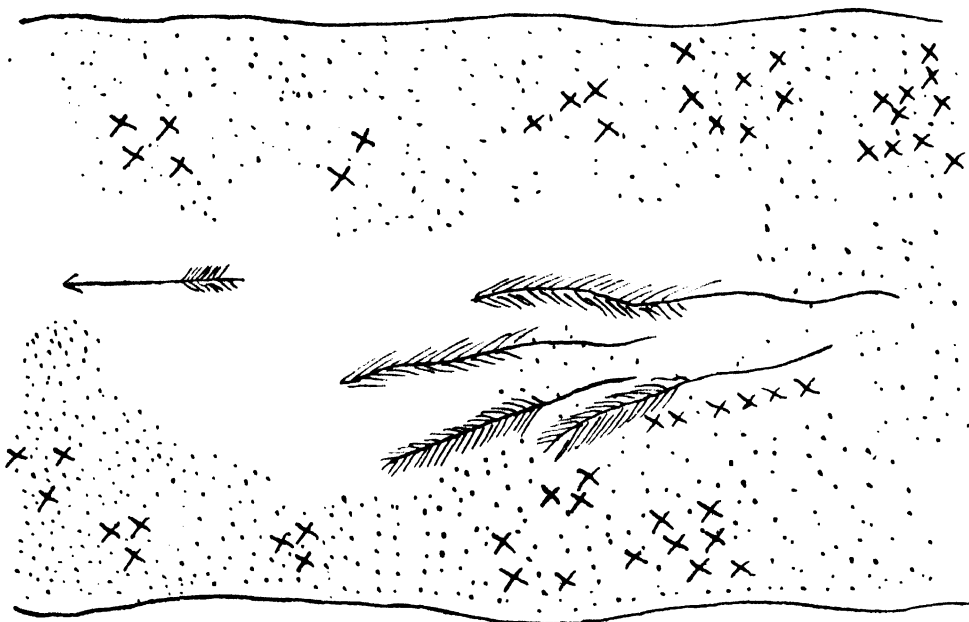
there were now two plants of *Potamogeton indicus* as well as two plants of *Potamogeton perfoliatus* (see Fig. 6).

On June 30, 1925, about 20 months after clearance, the silt was $2\frac{1}{2}$ to 3 inches deep. *Nitella* was decreasing and *Vallisneria* was increasing. The *Potamogetons* had made considerable growth, and were well rooted, showing that they had got necessary depth of silt for their establishment.

The above, although an isolated experiment, gives us at least some clue to the probable succession in this canal, viz.:

- (1) Deposit of fine silt.
- (2) Establishment of *Nitella* which causes further silt deposit.
- (3) Invasion by *Vallisneria*.
- (4) Invasion by *Potamogeton*.
- (5) Crowding out of *Nitella*; increase of *Vallisneria* and *Potamogetons*.

We may also be fairly certain that the last stage in this canal is decrease of *Vallisneria* and dominance of *Potamogeton* species.



Nov. 22 1924

xxx.. *Vallisneria spiralis* :::: *Nitella*
 // Potamogeton perfoliatus // *P. indicus*

FIG. 6. Chart of a rocky section of the Mutha Right Bank Canal, showing vegetation on November 22, 1924. Cf. Fig. 5.

A similar experiment was made at mile $12\frac{3}{4}$ on the Pravara Left Bank Canal during a closure in February 1924. A total length of 69 feet in a rocky section was then completely cleared of all silt and weed. Phot. 4 shows the

place just before clearing. The canal was revisited at the next closure on June 21, 1924, when silt was found deposited to a depth of from 3 to 6 inches in the cleared area. *Potamogeton pectinatus* had established itself thoroughly. Here there was certainly an exceedingly rapid deposition of silt and rapid growth of the invading species.

These two experiments indicate a very different condition in the two canals. The amazingly rapid increase of the silt deposit here is quite in keeping with the very heavy weed growth which occurs everywhere on this second canal.

SUMMARY.

1. An account is given of the aquatic weeds blocking three irrigation canals in the Bombay Deccan.
2. The presence or absence of weeds is determined by the deposition of silt.
3. The effect of silt in suspension is not proved. The three canals differ in amount of suspended silt, but the comparative poverty of aquatic flora in canals with more suspended silt can be better correlated with greater velocity and less deposition of silt.
4. An account is given of succession in one denuded area in a canal bed, and of immediate invasion by the climax species in the case of another.

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ASPECTS OF THE ECOLOGY OF CERTAIN FOSSIL CORAL REEFS

By W. J. ARKELL.

(*With Plates XIX—XXI, and two Figures in the Text.*)

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I. INTRODUCTION.

It is commonly known that during a part of the Upper Jurassic period coral seas covered much of the region now occupied by north-western Europe. The remains of the coral reefs, sandbanks and shell beds which were formed during this phase are known collectively as the Corallian formation, or sometimes as the Lusitanian. The outcrop of these rocks in England forms a chain of low hills running along the centre of the lowland tract floored by the Oxford and Kimeridge Clays, parts of which are designated the Vale of Blackmore, the Vale of the White Horse, the Vale of Aylesbury, the lowlands of Bedford, Huntingdon and Fenland, the Vale of Lincoln and the Vale of Pickering. The Corallian formation represents over most of this area a shallow, clear-water episode, sandwiched between two thick clay formations.

During the deposition of the Oxford and Kimeridge Clays the seas of northern Europe were relatively deep and muddy. The rich molluscan and brachiopod faunas of the Lower Oolite limestones were poorly represented, except by cephalopods and oysters, and there was a revival of the great marine reptiles, the Pliosaurus, Plesiosaurs and Ichthyosaurs, belonging to genera common in the Lias. The conditions were the very antithesis of those required for the growth of reef-forming corals.

Just as the clays of the Lower Lias are separated from those of the Upper by the marlstones, limestones, sands and ironstones of the Middle Lias, so the Oxford Clay is separated from the Kimeridge Clay by the Corallian limestones, sands and shell banks, denoting similarly a shallow-water episode, but this time peopled by widespread colonies of Anthozoa. Everywhere this change from the muddy conditions brought with it a new and richer fauna, of which the molluscan assemblages recall those of the Inferior Oolite and Cornbrash, while the corals take the position of importance held by the

Brachiopoda in those formations. The impoverished fauna of the succeeding Kimmeridge Clay has hardly a species in common with that of the Oxford Clay, but the Corallian fauna embodies some species from both.

The areas of coral-reef development in England were confined, with trifling exceptions, to (i) Yorkshire, (ii) the Oxfordshire-Berkshire-Wiltshire range, and (iii) Kent. The Kent rocks are known only from borings; and of the other areas the second is that in which coral reefs can be distinctly traced through the greatest number of consecutive periods, and is consequently of most importance from the point of view at present adopted.

The reefs are always thin, the thickness of actual corals being usually from 10 to 15 ft. and in no known instance exceeding 20 ft. They fall within the category of Fringing Reefs, to which all the Jurassic reefs of England and France belong. They take the form either of coral islands, separated by channels filled with shelly and detrital deposits, or of a true fringing reef, of no great width but many miles in length. At the period of maximum coral development both forms occurred, and the north-western shore of the land mass, which then occupied the site of the London basin, parts of the North Sea and the Ardennes, was fringed with almost continuous coral growth from Oxford to Calne, in Wiltshire.

II. THE SUCCESSION OF THE REEFS IN SOUTHERN ENGLAND.

Until recently the stratigraphical succession of the Corallian formation was very imperfectly understood. The leading authority has long been Blake

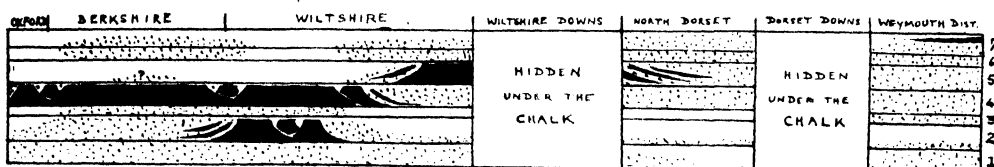


FIG. 1. Diagrammatic representation of the Corallian rocks along the outcrop in the South of England to show the horizontal and vertical distribution of coral reefs. Black = coral; Dotted = other deposits.

- | | | |
|-------------------------------------|---|--------------------------|
| 7. Iron ore and Ringstead Coral Bed | } | Upper Calcareous Grit. |
| 6. Sandfoot Grit and Clay | | |
| 5. <i>Trigonia clavellata</i> Beds. | } | Berkshire Oolite Series. |
| 4. Osmington Oolite Series. | | |
| 3. Bencliff Grit and Nothe Clay | | |
| 2. <i>Trigonia perlata</i> Beds | | |
| 1. Lower Calcareous Grit. | | |

The Ringstead Coral Bed of the Weymouth district may be derived from a destroyed reef formerly situated in the English Channel, but it is also possible that the parent reef still exists beneath the Cretaceous rocks to the north-east.

and Hudleston's *Corallian Rocks of England*, published in 1877¹. These writers separated from the principal mass of the reefs (i) a local development of corals in the Lower Limestones at Hackness, Yorkshire, which, they pointed out, was

¹ *Quart. Journ. Geol. Soc.* **33**, 1877, pp. 260-405.

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much older, and (ii) a small coral bed, 8 in. thick, near Weymouth, which they found to be considerably younger. The main reefs of Yorkshire and of Oxford, Berks and Wilts, however, were considered to be of one age and were classed together as "the Coral Rag." This classification has usually been adopted in the various Survey Memoirs and other works dealing with the areas concerned.

The writer has shown that rags of three distinct ages are embraced within the single county of Wiltshire, and that in consequence the term "the Coral Rag" is not permissible as a stratigraphical term without local qualification. Coral rag is, in fact, a facies rock which may be formed at any time, wherever conditions are suitable. A revised classification has been proposed for the Corallian rocks of England, based upon the sequence of non-coral-bearing deposits, into the terminology of which the local coral reefs of various ages do not enter. This sequence is as follows¹:

| | History of coral development |
|---|--|
| KIMERIDGE CLAY | Reefs extinct in England but still forming on the continent. |
| CORALLIAN: | |
| 5. Upper Calcareous Grit | Thin coral bed at Weymouth. |
| 4. <i>Trigonia clavellata</i> Beds | Coral reefs in S. Wilts and N. Dorset and at Upware. |
| 3. Osmington Oolite Series | Maximum development of coral reefs in Yorkshire, Oxfordshire, Berkshire, Wiltshire and Upware. |
| 2. Berkshire Oolite Series (including <i>Trigonia perlata</i> Beds) | Coral reefs in N. Wiltshire. |
| 1. Lower Calcareous Grit | Coral reef in Yorkshire; clays still being deposited on the continent. |
| OXFORD CLAY | Clays widespread over Europe. |

From this table it will be seen that before the Oxford Clay period had terminated on the continent, the clear-water conditions of the Lower Calcareous Grit prevailed over England and the first coral reef was already established in Yorkshire. Later, coral growth spread southward over England and the continent, where it survived into the Kimeridgian after becoming extinct in England.

III. THE CHANGING AND UNCHANGING FAUNAS.

The first manifestation of a coral reef of this period in England consisted of the corals *Thecosmilia annularis* (Flem.), *Thamnastraea concinna* (Goldf.), *Isastraea explanata* (Goldf.) and *Rhabdophyllia phillipsi* Edw., and was confined to the district about Hackness in Yorkshire². The field relations and stratigraphical position of this earliest reef and of the various parts of the succeeding "Coral Rag" of Yorkshire have not been determined with such precision as those of their equivalents in the South of England, though W. H. Hudleston in 1878 (*loc. cit.*) hinted that rags of several different ages might be represented.

¹ W. J. Arkell. *Phil. Trans. Roy. Soc. B.* Nov. 1927.

² See W. H. Hudleston. "The Yorkshire Oolites," Part II, Section 2. *Proc. Geol. Assoc.* 5, 414, 1878.

We will therefore proceed directly to a consideration of the South of England, which the present writer has recently studied in detail.

(a) *Reefs in the Berkshire Oolite Series.*

The lowest and oldest true reefs in the south occur in the Highworth district of Wiltshire, where they form a group of coral islets. This older coral rag may easily be distinguished from the later rag of the Osmington Oolite Series by the fact that a band of sand and clay, sometimes 10 or 12 ft. thick, separates the two, though the presence of two coral rags was not suspected until the district was mapped on the 25-inch scale by the writer in 1924-5. The coral islets occupy an area of the present outcrop limited to about four square miles and each islet is only a few fields in extent, though greater expanses may have been removed by denudation or may still lie hidden beneath later rocks.

The corals constituting these reefs belong to the following species, enumerated in order of importance: *Thamnastraea concinna* (Goldf.), *Thecosmilia annularis* (Flem.), *Thamnastraea arachnoides* (Park.), *Isastraea explanata* (Goldf.), *Montlivaltia dispar* (Phil.), *Comoseris* sp. nov. With them are always associated the echinoderms, *Cidaris* (*Paracidaris*) *florigemma* Phil., and *Cidaris* (*Plegiocidaris*) *smithi* Wright, as well as a select molluscan fauna, which may be conveniently spoken of as the "coral fauna."

CORAL FAUNA (MOLLUSCA). (See Plate XXI.)

Littorina muricata Sow.

Lima (*Plagiostoma*) *zonata* Ark.

Exogyra nana (Sow.).

Pecten (*Chlamys*) *nattheimensis* de Lor.

Lithodomus inclusus (Phil.)

Ostrea gregaria Sow.

These molluscs are not only almost invariably found in abundance among the corals, but, with the exception of the two oysters, they are scarcely ever found dissociated from corals. The two oysters are included because they are always, in this and the succeeding periods, very much more abundant in the vicinity of coral reefs than elsewhere. The *Lima* and the *Pecten* the writer has not in any single instance detected in any situation other than the interstices among reef corals, where they are abundant.

The isolated coral reefs of this age pass laterally into shelly limestones, the *Trigonia perlata* limestones. These limestones contain an echinoderm and a few species of molluscs which also occur in the coral reefs, namely *Nucleolites scutatus* Lamk., *Pseudomelania headingtonensis* (Sow.), *Pecten* (*Chlamys*) *splendens* Dollf., *Ctenostreon proboscideum* (Sow.), a *Plicatula*, and the two oysters already mentioned. The vast majority of the forms which characterise these limestones, however, take no part in the constitution of the coral rag. The most conspicuous groups are the *Cephalopoda*, of which a great variety occurs, and the genus *Trigonia*.

In the neighbourhood of Highworth, Wiltshire, some quarries show beds of rolled corals intercalated among the shelly limestones, and at Kingston

Bagpuize in Berkshire, ten miles from the nearest reef now preserved, small fragments of *Thecosmilia* and *Isastraea* have been found. East of this the corals completely die out and throughout Berkshire the non-coralline fauna occurs in its greatest profusion and purity. The following is a list of the most abundant and characteristic species of the shelly limestones, none of which is in any way characteristic of the reefs of equivalent age, even though solitary specimens may sometimes be found in association with them:

| | |
|---|---|
| <i>Trigonia perlata</i> Ag. | <i>Lima</i> (<i>Limatula</i>) <i>elliptica</i> Whit. |
| Ditto, var. <i>hudlestoni</i> Lyc. | <i>Ostrea</i> (<i>Gryphaea</i>) <i>dilatata</i> Sow. |
| <i>T. meriani</i> Ag. | <i>O. quadrangularis</i> Ark. |
| <i>Trichites giganteus</i> Quenst. | <i>Perna mytiloides</i> Lamk. |
| <i>Corbicella laevis</i> (Sow.) | <i>Pholadomya canaliculata</i> Roem. |
| <i>Cucullaea contracta</i> Phil. (long var.) | <i>P. protei</i> Brong. |
| <i>Arca aemula</i> Phil. | <i>Pleuromya tellina</i> Ag. |
| <i>Gervillia aviculoides</i> Sow. | <i>Pteria</i> (<i>Oxytoma</i>) <i>expansa</i> (Phil.) |
| <i>Astarte ovata</i> Smith | <i>Pseudomonotis ovalis</i> (Phil.) |
| <i>Pecten</i> (<i>Camptonectes</i>) <i>lens</i> Sow. | <i>Sowerbya triangularis</i> (Phil.) |
| <i>P. (Chlamys) fibrosus</i> Sow. | <i>Unicardium apicilabratum</i> Etall. |
| <i>P. (Chlamys) splendens</i> Dollf. | <i>Pseudomelania heddingtonensis</i> (Sow.) |
| <i>P. (Entolium) solidum</i> (Roem.) | <i>Natica</i> (<i>Ampullina</i>) <i>arguta</i> Phil. |
| <i>Lima</i> (<i>Plagiostoma</i>) <i>rigida</i> (Sow.) | <i>Pleurotomaria reticulata</i> Sow. |
| <i>L. (Plagiostoma) mutabilis</i> Ark. | <i>Bourguetia striata</i> (Sow.) |
| <i>L. (Plagiostoma) laeviuscula</i> (Sow.) | <i>Cephalopoda</i> (abundant). |

The *Trigoniae* of the *perlata-hudlestoni* type occur massed together in great profusion at Marcham and Kingston Bagpuize, but the valves are never united. (Compare Plate XIX, Phot. 2.)

(b) Reefs in the Osmington Oolite Series.

Earth movements next caused the Wiltshire coral islands to be covered with beds of clay and sand and the equivalent shelly limestones in parts of Dorset, Berkshire and Wiltshire to be entirely removed. A period elapsed sufficiently long for the deposition of 80 ft. of clay and sand in south Dorsetshire (the Nothe Clay and Bencliff Grit). When coral growth was resumed the conditions were more favourable than previously and reefs spread far and wide over the shelly beds and the clays and sands of the preceding period. A luxuriant fringing reef grew from Oxford to Calne, in Wiltshire. In the neighbourhood of Oxford and at Purton, where anticlinal uplifts had shallowed the sea bed, archipelagos of coral islands spread outwards from the reef¹.

The fauna of the widespread coral rag of this age is identical with that of the last except that three new corals made their first appearance in the south of England, *Comoseris irradians* Edw., *Stylina tubulifera* (Phil.) and *Rhabdophyllia phillipsi* Edw., together with some rare echinoids, e.g. *Diplopodia versipora* (Phil.) and *Hemicidaris intermedia* (Flem.). The first coral is practically confined to a local station near Purton and the other corals and

¹ Vide Darwin: "It follows...that where the sea is very shallow, as in the Persian Gulf and in parts of the East Indian Archipelago, the reefs lose their fringing character and appear as separate and irregularly scattered patches, often of considerable size." *Coral Reefs*, 3rd edition, 1889, pp. 77-78.



Phot. 1. Section at Purton, Wilts., showing lenticular sheets of corals (*Thamnastraea concinna*), growing upon and covered by a débris of broken corals and shells. At the base of the quarry the débris is partially cemented into bands of hard white limestone.



Phot. 2. Slab of fossil shell-bank from the *Trigonia clavellata* beds of the Weymouth district. (In the British Museum.) (Much reduced.)

echinoids are too rare to affect the general features of the association. The third coral appeared in the first Hackness reef in Yorkshire, so its presence in the Berkshire Oolite reefs may be revealed by further collecting. The rest of the "coral fauna" is identical, and it is usually impossible to distinguish the new reefs from their predecessors from internal evidence alone.

With the advent of coral growth on this scale a new feature made its appearance, a calcareous deposit formed almost entirely of the débris of the reefs and their associated shells, ground down by the waves. Currents collected such material and piled it up to great thicknesses near Oxford (at Wheatley and Wootton) and at Purton. The only reef mollusc having a shell sufficiently small and strong to escape destruction by the waves and to be moved unbroken by the currents was *Exogyra nana*, which accumulated in immense numbers among the débris. Certain bands are largely composed of broken *Cidaris* spines, while unbroken tests of a large *Pygaster* and *Nucleolites scutatus* indicate that these echinoids lived among the accumulating débris, for they are not only unbroken but unrolled.

Towards Calne the reefs die out. They first alternate with and finally pass into white oolites with many echinoderms and abundant *Pecten* (*Chlamys*) *qualicosta* Etall. At Calne these constitute the Calne Oolite or freestone; they form the principal feature of the Corallian formation through the rest of Wiltshire, emerging from below the Chalk in North Dorset as the Marnhull and Todber Freestone and thickening in the Weymouth district as the Osmington Oolite Series. At certain horizons *Pecten qualicosta* and *Pecten fibrosus* are abundant, but usually the oolites cannot be termed shelly; there is no comparison with the shallow-water shell banks of the preceding Berkshire Oolite period. A probable explanation of this is that the whole of that part of the shallow-water region, the deposits of which are preserved and exposed, was covered by coral reefs and their associated débris, and that we are here dealing with oolites formed at a greater depth and beyond coral influence.

Of the coral reefs of this period we can say, then, that the fauna was essentially the same as that of the older reefs, except that a great horizontal expansion was accompanied by the appearance in certain localities of a few rare species, not met with in the previous restricted reefs. Of the non-coral fauna we can only note the preponderance of one new species, *Pecten qualicosta*, in such numbers as to dominate the fauna, and the vanishing of practically the whole of the long list characteristic of the shell banks of the preceding period.

(c) *Reefs in the Trigonina clavellata Beds.*

At Steeple Ashton, Wiltshire, there is a coral rag which has long been famous for the wealth and beauty of preservation of its corals. The significant fossil *Trigonina clavellata* Park. (*T. bronni* Ag.) has been recorded from it, and it moreover rests upon the top of the white Calne Oolite, representing the Osmington Oolite Series. It is therefore younger than the reefs that have

just been described. This has long escaped observation, in spite of the fact that the corals are in a much finer state of preservation and include some species not found elsewhere in England. These new corals are *Calamophyllia stokesi* Edw., *Cladophyllia conybeari* Edw.¹ and *Goniocora socialis* (Roem.) While they are significant, just as is the single record of *Trigonia clavellata*, for the dating of the coral reef, they are again not sufficiently common to be of importance in modifying the general aspect of the fauna. The predominant corals are still the same species as those which built the two earlier reefs and the whole molluscan and echinoid association has remained essentially unchanged.

If the Steeple Ashton reef, which is more southerly than any previous coral growth in England, ever grew between Westbury and Cambridge, it was removed prior to the deposition of the Upper Calcareous Grit. An unconformity at this horizon and another at the base of the Kimeridge Clay have swept away much of the evidence for the later Corallian history in the middle and north of England.

How far south the reef extends is unknown, for soon after making its appearance it passes out of sight beneath the Chalk downs. When the Corallian rocks reappear from beneath the Chalk on the north side of the Vale of Wardour, the Osmington Oolite Series is overlain by shallow-water shelly beds, full of *Trigoniae* and resembling, but only in general appearance, the *Trigonia* beds of the Berkshire Oolites. These shelly beds contain here and there a high proportion of rolled corals and they certainly lie on the same horizon as the Steeple Ashton reef, which may therefore be presumed to extend for a considerable distance beneath the Chalk towards the Dorset border. The shelly beds may be studied in many exposures through North Dorset, at Silton, East Stour, Stour Provost and elsewhere. They contain a decreasing proportion of corals southward and they soon assume the ordinary characters of the *Trigonia clavellata* beds of the Weymouth district, of which they form the northerly extension. (See Plate XIX, Phot. 2.)

A closer examination shows that the resemblance to the Berkshire Oolite shell beds is purely superficial. The same type of deposit is here repeated in association with an almost identical reef; but while the coral and mollusc association of the reef is specifically the same as that of preceding reefs, there is in these shell beds hardly a single mollusc of importance which was met with in the earlier shell beds. The faunal assemblage has completely changed. Instead of the large *Trigoniae* of the *T. perlata* and *T. huddlestoni* type we find the smaller *T. clavellata* (or *T. bronni*), often with the valves united. The large *Astarte ovata* has given place to hundreds of the little *Astarte polymorpha* and *A. supracorallina*; the curved *Gryphaea dilatata* has been superseded by the flat oyster, *Ostrea sowerbyi*; and so on through almost the

¹ There is a record of this by Phillips from Cumnor, which, if reliable, indicates that it also occurs in the Osmington Oolite rag, but extremely rarely.

whole list. The following are the principal species from the *Trigonia clavellata* beds (rare species are again not included):

Trigonia clavellata Park.
T. meriani Ag.
Cucullaea contracta Phil. (short var.)
Astarte supracorallina d'Orb.
A. polymorpha Contj.
Lucina goldfussi Desh.
Pleuromya tellina Ag.
Ceratomya excentrica (Roem.)
Ceromyopsis striata (d'Orb.)
Goniomya v-scripta Sow.

Gervillia aviculoides Sow.
Perna mytiloides Lamk.
Pecten (Chlamys) qualicosta Etall
P. (Chlamys) superfibrosus Ark.
Ostrea sowerbyi Bronn (= *deltoidea* Sow.)
O. (Lopha) solitaria Sow.
Mytilus pectinatus Sow.
M. varians Roem.
Alaria seminuda Heb.
Nerinea fasciata Voltz.

Although, in addition to these, several species from the *Trigonia perlata* beds occur, they are here only rare, occupying a very subordinate position in the assemblage.

IV. A RECENT ANALOGUE IN THE RED SEA.

The northern parts of the Red Sea and the adjoining coasts of the Gulf of Suez and the Gulf of Akaba are skirted with fringing reefs having many features in common with those in the European Jurassic. They have been several times described, notably by Ehrenberg¹, by Klunzinger² and by Barron and Hume³, but never from the point of view at present under consideration. By singular good fortune the present writer had the opportunity of visiting the region early in 1927, when working with Dr K. S. Sandford on the Pleistocene problems of Egypt for the Oriental Institute of the University of Chicago. To Professor James H. Breasted, Director of the Institute, he is indebted for permission to publish the results obtained *en passant* while engaged on the work of the Institute.

The area observed was a stretch of coast about 20 miles in length near Qosseir, in lat. 26° N., on the western shore of the Red Sea. The coral reefs of this region are the most northerly of any importance at present growing in the world. The coast has been subjected to periodic elevation during Pleistocene times and a series of rock platforms has been cut between the successive elevations. These platforms run horizontally for many miles along the coast and they are cut in old tilted barrier reefs and gravel fans of Middle and Upper Miocene and Pliocene age, often dipping seawards at angles of as much as 40°. On the lowest platform there is a well-preserved semi-fossil fringing reef of late Pleistocene date, raised from 20 to 30 ft. above present sea level, and strictly analogous with that at present forming in the sea. This raised reef is a widespread feature and is of equal importance on the coast of Sinai⁴.

¹ "Über die Natur und Bildung der Coralleninseln und Corallenbanke im Rothen Meere." *Abh. k. preuss. Akad. Wiss. Berlin*, 1832 (1834).

² *Bilder aus Ober-Aegypten, der Wüste und dem Roten Meere*. Chapter VI. Stuttgart, 1876.

³ *Topography and Geology of the Eastern Desert of Egypt*. Egyptian Survey Department, Cairo, 1902, p. 135.

⁴ Walther, J. K. *Die Korallenriffe der Sinaihalbinsel*. *Geol. und biol. Beobachtungen* Leipzig, 1888, p. 484.

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The average width, both of the recent and of the Pleistocene reef, is from 100 to 300 yards, and the thickness of the coral is probably rarely more than 15 or 20 ft. An indeterminate part of the width of the recent reef on the shoreward side does not belong to the present epoch of coral growth but is really a marine platform cut in the old raised reef, of which the parts above present sea level are still receding behind a small vertical cliff. Coral growth probably has not, therefore, proceeded so long since the last uplift as between the two preceding uplifts, when the raised reef was formed.

The corals building the reef are too numerous to mention¹. In their various forms the principal species resemble the *Hexacoralla* of the Jurassic, though the assemblage is much richer. The massive *Isastraea*, *Thamnastraea* and *Comoseris* are replaced by *Goniastraea*, *Orbicella*, *Solenastraea*, *Acanthastraea*, *Prionastraea*, etc. and the branching *Thecosmilia* by *Stylophora* and *Madrepora*. It is, of course, only in their growth forms, a superficial feature having no connection with classification and yet so striking to the eye, that they resemble the early corals of the Jurassic; the genera and even families are widely different. It is only such a parallel, it must be clearly understood, as can be drawn between the individual corals in the modern reefs and their Jurassic predecessors in Europe as between the reefs themselves. There are many points of difference, of which perhaps the most important are the parts played by calcareous Algae (*Lithothamnium*) and by Foraminifera. Nevertheless, the coral seas and their fringing reefs of the Jurassic, regarded as an ecological unit, were essentially analogous with the Red Sea to-day, and the same principles which we have discerned in the preceding pages are in operation in the neighbourhood of Qosseir.

By collecting the shells either living among or lying fresh in the interstices between the corals at low tide, a definite "coral fauna" was obtained. Besides the echinoderms, which included Holothurians, Asteroids, Ophiuroids and Echinoids (principally *Tripneustes* and *Echinometra*) a certain molluscan suite was always obtained, of which the number of species was few, but the individuals numerous.

It was found that the storm beaches inside the coral reef, composed entirely of corals and shells cast up during tempests, contained besides these species a large number of others not found living on the reef. The alien species, in fact, far outnumbered the coral-dwelling species.

If, then, these species were not torn from the reef itself with the corals and the coral-dwelling shells, it seems necessary to suppose that they came from outside the reef, where this other association may be supposed to be living out of reach of normal wave action. Opportunity was not afforded of putting this to the test by dredging, but that wave action on this coast during exceptional storms is exceedingly strong is shown by the large size of some of the masses of coral torn from the reef and cast up high on the storm

¹ Ehrenberg (*op. cit.* p. 46) records 120 species from the Red Sea.



The 25 ft. 30 ft. RAISED REEF, growing upon eroded hummocks and ridges of *Lithothamnium* limestone, behind the salt marshes, Old Qossier Harbour.



PLEISTOCENE RAISED SHELL-BANK exposed on an elevation in the salt marshes, Old Qossier. The shells visible are *Circe lentiginosa*, *Circe pectinata*, *Anadara antiquata*, *Glycymeris pectunculus* and *Cardium leucostomum*.

[illegible]

Generally, however, the depth at the same distance from the shore does not exceed 30 fathoms, showing that a comparatively shallow shelf exists between the shore and the deep water. Here and there shoals exist upon this shelf, reducing the depth to one-half. Such shoals are usually found opposite the

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mouths of wadies, where their presence may be attributed to the deposition of gravel and mud by rivers in Pleistocene times, but they are also due sometimes to other causes, probably the rearrangement of the same material by currents, for such a shoal appears off the headland three miles north of the "Boat Harbour" marked on the map. This bank probably supplied much of the material collected near old Qosseir, immediately opposite which deep water approaches close to the shore.

The commonest species of the non-coral association collected on the storm beaches, are the following:

COMMON SPECIES OF SHELLS ABOUNDING ON THE STORM BEACHES NEAR QOSSEIR, BUT NOT FOUND ALIVE ON THE REEF.

| | |
|--|---------------------------------------|
| <i>Tellina rugosa</i> Born. | <i>Pterocera bryonia</i> Gmelin |
| <i>Arca</i> (<i>Anadara</i>) aff. <i>antiquata</i> Linn. | <i>Strombus tricornis</i> Lamk. |
| <i>Cryptodon globosa</i> (Forsk.) | <i>Fusus polygonoides</i> Lamk. |
| <i>Hemicardium auriculum</i> (Forsk.) | <i>Cerithium erythraeonense</i> Lamk. |
| <i>Asaphis deflorata</i> (Linn.) | <i>Conus monachus</i> Linn. |
| <i>Dolium variegatum</i> Lamk. | <i>C. miliaris</i> Hwass |
| <i>D. perdix</i> (Linn.) | <i>C. flavidus</i> Lamk. |
| <i>Tectus dentatus</i> Forsk. | <i>C. nussatella</i> Linn. |
| <i>Lampusia pilearis</i> (Lamk.) | <i>Cypraea arabica</i> Linn. |
| <i>Turris garnonsi</i> Reeve | Cuttlefish pens (from the open sea). |

Turning now to the raised Pleistocene reef, we find some interesting facts. Many sections are visible where the reef may be seen growing upon rounded hummocks of old Pliocene *Lithothamnium* limestone—a fine example of an eroded surface. Continuous sections also are open for collecting for miles along the coast, where the large clams (*Tridacna gigas*) lie still embedded in the corals, 30 ft. above the sea. From these sections it is apparent that the constitution of the old reef was almost exactly the same as that of the recent reef and, in particular, the *mollusca* found in the interstices among the corals are in the main identical.

THE "CORAL FAUNA" (MOLLUSCA) COLLECTED COMMONLY IN THE RAISED PLEISTOCENE REEF AND THE RECENT REEF NEAR QOSSEIR¹.

| | |
|---|--|
| <i>Codakia exasperata</i> (Reeve) | <i>Strombus fasciatus</i> Born. |
| " <i>Venus</i> " <i>reticulatus</i> Linn. | <i>Canarium gibberulum</i> (Linn.) |
| <i>Septifer excisus</i> (Wiegmann) [only] | <i>Turbo radiatus</i> Gmelin |
| <i>Cardita calyculata</i> (Lamk.) (seen in raised reef) | <i>Bulla ampulla</i> Linn. |
| <i>C. (Beguina) gubernaculum</i> Reeve (seen in raised reef only) | <i>Vasum cornigerum</i> (Lamk.) |
| <i>Barbatia obliquata</i> (Wood) | <i>Conus omaria</i> Hwass. |
| <i>B. fusca</i> (Brug.) | <i>Nerita albicilla</i> Linn. |
| <i>B. helblingi</i> (Brug.) | Chitons. |
| <i>Arcopagia scobinata</i> (Linn.) | Following abundant on the modern reef but not actually seen alive: |
| <i>Tridacna gigas</i> Linn. | <i>Cypraea turdus</i> Lamk. |
| <i>Chama nivalis</i> Reeve | <i>C. Vitellus</i> Linn. |
| <i>C. cornucopiae</i> Reeve | <i>Terebra consobrina</i> Desh. |
| <i>Spondylus aculeatus</i> Chem. | <i>Natica melanostoma</i> (Gmelin) |
| <i>Clanculus pharaonius</i> (Linn.) | |

¹ Greatest importance is attached to the Polécypods, for the shells of Gastropods not found living on the reef are fetched from the beach in thousands by hermit crabs. It is also possible that live specimens of the four species of *Conus* enumerated in the list from the beaches were overlooked on the reef, where they are not easily seen, owing to growths of Algae covering the shells.

Besides the invertebrata mentioned, many kinds of small fish are conspicuous in and about the modern reef, but their remains are very rare in the raised reef. Bones of Teleosts are equally rare in the fossil reefs of the Jurassic, where, however, fin spines of Elasmobranchs are fairly numerous. It seems probable that few small reef fish die a natural death, most of them being eaten by the sharks, which come on to the reef with the rising tide and may be seen in large numbers scouring the warm waters for food.

Opposite the mouths of wadies, which were important watercourses in Pleistocene times, wide bays or gaps interrupt the continuity of the raised reef, while only a narrow break admits the waters of the rare *seils* of the present climate to pass through the modern reef. These bays are now flooded by flat salt marshes barely above present sea level. Round the edges the old sea bed rises a few feet above the salt marshes and the old bottom deposits may be seen, banked against the ridges on which the corals grew. Here the spectacular shell banks generally known by the misleading name of "raised beaches" are found (Plate XX). Those examined seemed to be not raised beaches, but true shell banks, probably formed under from 20 ft. to 30 ft. of water. They preserve the fauna of those parts of the sea bed uncolonised by corals, and it is a fauna almost exclusively molluscan. Near the edges there is a certain admixture with the coral fauna, but this is mostly due to gravity, the reefs being on a higher level. Where there is no such contamination (and the shell banks are heaped over vast areas in a state of purity) two important facts are observed: first, the assemblage is entirely different from that of the coral reef; secondly, *it is different from the non-coral assemblage of the modern beach.*

PRINCIPAL SPECIES FORMING THE PLEISTOCENE SHELL BANKS NEAR QOSSEIR.

| | |
|----------------------------------|--------------------------------|
| Arca (Anadara) radiata Reeve | Diplodonta rotundata (Mont.) |
| A. (Anadara) antiquata Linn. | Macrocallista florida (Lamk.) |
| Circe pectinata (Linn.) | Dosinia radiata (Reeve) |
| C. crocea (Gray) | Paphia sulcaria (Lamk.) |
| Cardium leucostomum (Born.) | Venericardia cumingi (Desh.) |
| Lutraria intermedia (Reeve) | Glycimeris pectunculus (Linn.) |
| Brachydontes variabilis (Krauss) | Ostrea cucullata Born. |
| Cerithium ruppelli Philippi | O. gryphoides Schloth. |
| C. scabridum Philippi | Terebralia palustris Linn. |
| Pirenella conica (Blainville) | |

In spite of the differences, then, between the old fringing reefs of the English Jurassic and those of the Pleistocene and Recent of the Red Sea, their relation to the contemporary shell beds is the same. The desert conditions obtaining on the coast of Egypt enable us to trace out step by step, unobscured by vegetation, the changes from reef to shell bed and from reef to detrital deposit which we are obliged in England to piece together from evidence gleaned in scattered quarries.

Since the molluscan assemblage in the successive reefs remained practically constant, the question at once arises, to what agency were the changes in the contemporaneous non-coralline or "shelly" assemblages due?

The observations made on the Red Sea coast were confined to an area 20 miles in length. If we go farther afield we find that the Pleistocene shell bank species, the greater number of which have now disappeared from the vicinity of Qosseir, are not extinct. On the contrary, every one of the 20 species enumerated is still living, either in other parts of the Red Sea or in the Gulfs of Suez and Akaba, the Indian Ocean, or still more distant waters. The Pleistocene assemblage of the Qosseir shell banks is no more, but the individual species still take part in other assemblages elsewhere, while a new assemblage has taken their place at Qosseir.

The answer to our question is apparent. The changes in the non-coralline assemblages are due, not to evolutionary modification or extinction of the original species, but to migrations. Thus, while we find at Qosseir a geological succession of two faunas in the raised shell banks and the present sea, the raised shell banks are homotaxial with shell banks now forming in distant regions such as the Gulf of Akaba, the shores of Zanzibar, the Philippine Islands or Australia¹.

V. DISCUSSION OF THE CONCLUSIONS AND THEIR BIOLOGICAL AND GEOLOGICAL BEARING.

In the coral seas, past and present, which we have examined, it has been noticed that the reef and its immediate vicinity harbours a mixed assemblage of echinoderms and molluscs peculiar to that particular habitat. It has often been pointed out that the echinoderms, both Echinoids and Holothurians, contribute materially to the fabric of the reef, both by the accumulation of their hard parts after death and by the manufacture of calcareous ooze during life. Thus they seem, in a sense, an integral part of the reef, regarded as a growing mosaic of life forms, for which the calcareous skeletons of the Anthozoa and the Algae provide a framework. Certain molluscs, such as *Lithodomus*, are especially adapted to bore into this framework, but the presence of the other types, belonging to widely diverse families, is less easy to account for. The reasons why, for instance, *Venus reticulatus* and *Codakia exasperata* elect to live on the reefs of the Red Sea would form an interesting subject for biological research, and the results might throw some light on the problem of why such shells as *Lima zonata* and *Pecten nattheimensis* apparently never lived off the Jurassic reefs, while many closely allied species showed no such peculiarity. As is suggested by Pl. XXI, the only apparent character which all the reef-dwelling lamellibranchs have in common is a certain roughness of surface ornament.

For the present we can only state that the molluscan fauna of a coral reef, while showing no obvious adaptation to or suitability for its surroundings,

¹ The present-day distribution of most of the species may be found in R. Bullen Newton's "Pleistocene Shells from the Raised Beach Deposits of the Red Sea," *Geol. Mag.* N.S. Dec., iv, 7, 1900, pp. 500-514, 544-560.

seems to form a distinct assemblage from that living contemporaneously in the surrounding seas; and that, although the two assemblages may contain closely related species, they seem to remain to a certain extent mutually exclusive.

Secondly, by studying three successive Jurassic coral reefs and the associated shell beds in England and two similar Pleistocene—Recent stages on the Red Sea, it was established that, while the reef dwelling assemblage tends to remain constant, the associated bottom dwelling assemblage changes with each successive set of earth movements. In other words, the age of any fossil coral reef can only be determined by tracing it laterally into the associated non-coralline deposits.

Now coral reefs are a rare abnormality in the marine geological strata, which are primarily composed of a succession of non-coralline or "normal" deposits, which must be likened rather to our shell beds, though they are not always so fossiliferous. The rapid vertical change which the assemblages undergo through the formations, with a lack of transitional forms between the successive species, has always been the cause of the want of conviction with which most geologists view the evolutionary lines that have been traced through the strata. Enormous lapses of time have to be postulated, during which each successive fauna evolved from its predecessor and the intermediate forms or "connecting links" were swept away.

The coral reefs throw strong light on this problem. They provided refuges of constant environment for the species dwelling among them, while earth movements modified the surrounding sea bed, introducing colder or warmer currents or opening up new channels for migrations by setting up or removing barriers. Consequently the species inhabiting the reefs remained in one locality so long as the corals gave them their protection; the bottom dwelling species were driven out at each successive oscillation and their places occupied by incoming species already evolved and better adapted to the new conditions.

If we wish to trace the evolutionary history of a species we can most conveniently achieve our purpose by studying a succession of coral reefs, in which the species has been "fixed" geographically. The process of evolution is found to be very slow in comparison with the rapid changes suggested by the ever varying assemblages of the normal bottom deposits. To trace the history of such species it would be necessary to follow them all over the world, and we could never tell whither their migrations, impelled by ever changing conditions, had led them.

In short: first, it would seem to be wrong to seek to derive such a species as, for instance, *Trigonia clavellata*, from the earlier and underlying *Trigonia perlata*. The Mollusca in the coral reefs, which we can keep under observation through a series of rocks representing the same passage of time, undergo no comparable changes—in fact they show no apparent modification whatever. Secondly, we are warned once again of the danger of attaching too much

importance to the occurrence of the same species of fossils in widely separated regions, utilising them for minute correlation of the rocks in which they are embedded. If we could study a fifth as much of the Jurassic deposits with their fauna as we know of the fauna of the seas of the modern world, we should probably find that the principle of homotaxis expounded by Thomas Henry Huxley was as operative in Jurassic times as it is at the present day.

If, then, there is reason to believe that the immediate progenitors of a species are not usually to be found among their nearest allies underlying them in the rocks, but rather in the deposits of other regions, probably still covered by the oceans, and that such deposits which, if they were accessible, would be considered synchronous are really homotaxial, then a large body of geological speculations would seem to be without legitimate scientific basis.

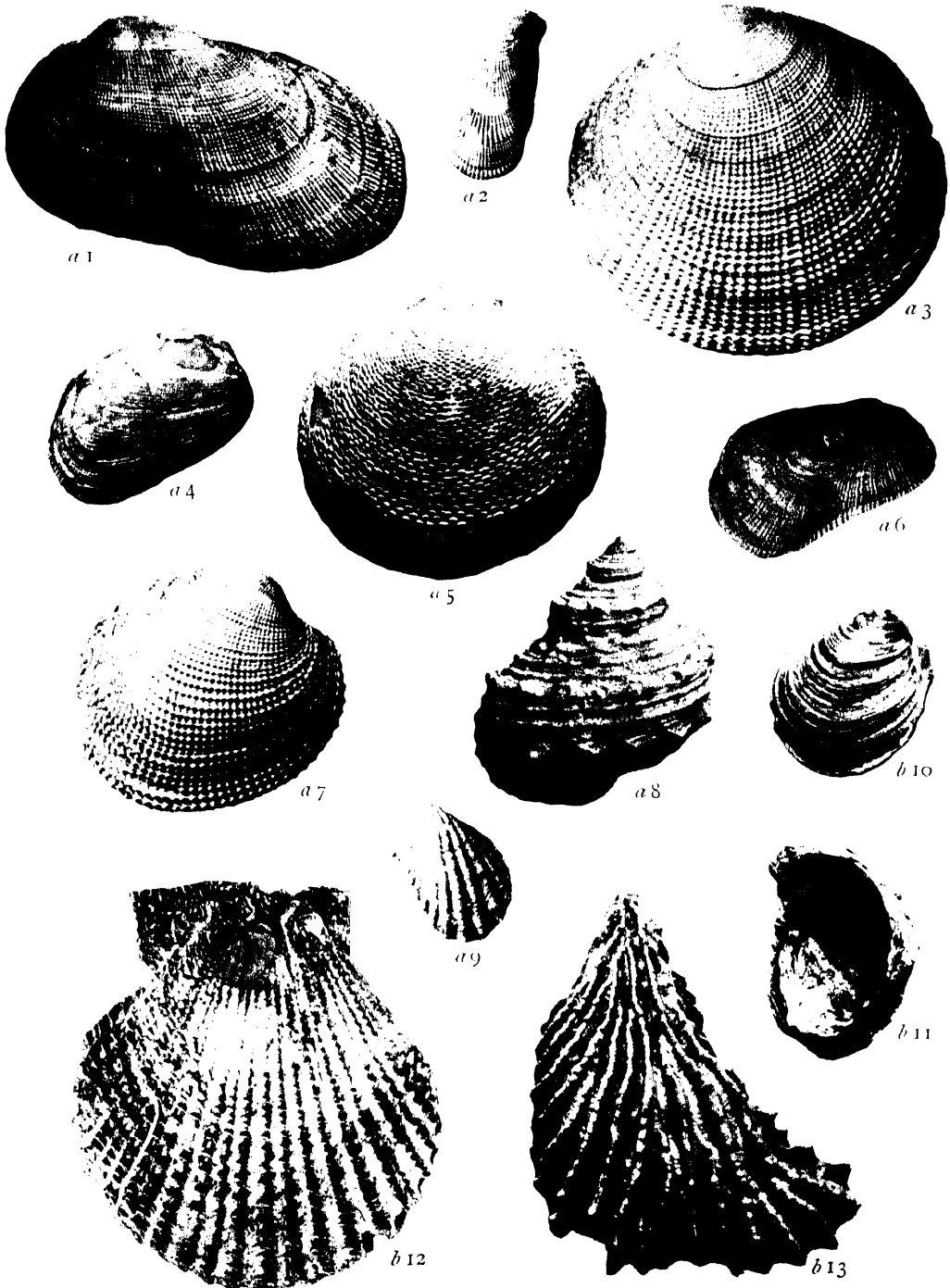
In the current volume of the *Quarterly Journal of the Geological Society*, for instance, we read the following passage:

"The Ammonoid horizons of the Cornbrash are then considered, and the divisions of Cornbrash time on the basis of Brachiopods and of Ammonoids are compared. Further, the Cornbrash and the Inferior Oolite are compared on these bases, the conclusion being reached that, either the Cornbrash Brachiopoda must have evolved three or four times more rapidly than those of the Inferior Oolite, or else that, if the time value of Brachiopod species be the same in the Cornbrash as in the Inferior Oolite—and there is every reason that it should be—then the Cornbrash must have taken in deposition a time far in excess of that of the Middle and Upper Inferior Oolite, with all its numerous Ammonoid hemerae¹."

This passage is taken from the summary of a paper in which the theme is elaborated at considerable length. It is typical of much somewhat loose geological thought, which arbitrarily assumes that each of the successive faunas in an observed series of rocks is evolved from its underlying predecessors. Only if predecessors be confused with progenitors is it truly dogmatised that the number of contained faunas is the criterion of the time taken for the formation of a series of deposits. If we explain the changes of fauna as due to migrations, however, no such artificial difficulties stand in our way.

Migrations result from various causes, of which the most potent have already been mentioned, and they certainly could not be expected to occur with any degree of regularity, or even of universality. The "time value" of the successive faunas, in fact, is probably not the same. By invoking the aid of migrations, not only are we relieved of the onus of assuming that 20 ft. of Cornbrash took as long to form as 200 ft. of Inferior Oolite, but also the age-old problems of incomplete evolutionary lines and "missing links" cease to provide a war cry for the fundamentalists.

¹ "Some Faunal Horizons in Cornbrash." *Quart. Journ. Geol. Soc.* **83**, April 1927, p. 29.



REEF-DWELLING MOLLUSCA; *a.* from the Red Sea Coast, Qosseir; *b.* from the Middle Jurassic reefs of the south of England. For identification see p. 149.

ARKELL.—ASPECTS OF ECOLOGY OF CERTAIN FOSSIL CORAL REEFS

Face p. 149

ACKNOWLEDGMENTS.

The indebtedness of the writer to Professor J. H. Breasted has already been mentioned in connection with the section dealing with the reefs of the Red Sea. The matter contained in this section was discussed on the ground with Dr K. S. Sandford, who helped to collect the material and contributed many valuable observations and criticisms. Without his help and encouragement it is doubtful if the paper would have been written, but the author alone takes all responsibility for the statements made and the views expressed. Mr O. H. Little, of the Geological Survey of Egypt, is also to be thanked for fruitful consultation concerning the Red Sea coast at Qosseir, with which he is personally acquainted. Mr J. R. Le B. Tomlin has very kindly revised the lists of Red Sea shells and identified some of the species. The map is reproduced by the courtesy of the Royal Geographical Society from the Admiralty Charts.

EXPLANATION OF PLATE XXI.

Mollusca common in the Pleistocene and Recent Reefs near Qosseir. *a. 1. Barbatia fusca* (Brug.) *a. 2. Septifer excisus* (Wiegmann). *a. 3. Codakia exasperata* (Reeve). *a. 4. Cardita (Beguina) gubernaculum* Reeve. *a. 5. Arcopagia scobinata* (Linn.). *a. 6. Barbatia obliquata* Wood. *a. 7. "Venus" reticulatus* Linn. *a. 8. Turbo radiatus* Gmelin. *a. 9. Cardita calyculata* (Reeve).

Mollusca common in the Corallian Reefs of Southern England. *b. 10. Lima (Plagiostoma) zonata* Arkell. *b. 11. Exogyra nana* Sowerby. *b. 12. Pecten (Chlamys) nattheimensis* de Loriol. *b. 13. Ostrea gregaria* Sowerby.

NOTES ON THE TUNDRA OF RUSSIAN LAPLAND

By R. RUGGLES GATES.

(*With Plates XXII and XXIII.*)

HAVING been invited by Professor N. I. Vavilov, Director of the Bureau of Applied Botany and Plant Breeding in Leningrad, to visit the plant breeding stations of Russia, I availed myself of the opportunity in the summer of 1926. My observations on the vegetation in the far North were made incidentally during a short visit to the Plant Breeding Station at Khibiny, which is the most northerly plant breeding laboratory in the world.

I left Leningrad, August 24th, 1926; and travelled north by train two days to Khibiny, past Lake Onega and the White Sea, into the Kola Peninsula, through a country of lakes, woods and swamps, which had been heavily glaciated, and was much like parts of northern Canada. Many plant species are the same as in Canada, and many of the common plants are rarities in the British flora, often found only in the Highlands of Scotland or in the north of England. Many of the species are circumpolar in high latitudes, and a large number bear the name of Linnaeus himself. The distance from Leningrad to Khibiny is nearly 1000 miles.

Dr Eichfeld, Director of the Plant Breeding Laboratory at Khibiny, came down to Leningrad to meet me and take me north. He was an Esthonian and spoke German fluently, so we had no language difficulty. He lives at the Khibiny Laboratory from April to November and spends the winter in Leningrad. The Laboratory is one of many in different parts of the vast Russian territory, controlled from the central Bureau in Leningrad. From this Bureau varieties of agricultural plants are sent out for testing to all these stations, and many valuable comparative results are being accumulated. Their mention here is not out of place, because they have, particularly in this instance, an ecological as well as a genetical bearing; for the comparative effects of the great range of climates to be found within Russian territory upon a wide range of identical crop plants are being determined, and in the extreme conditions of the North these climatic effects are most marked.

The site of the Laboratory seems to have been well chosen, since, while in the tundra, it is considerably sheltered by the surrounding mountains, being on the eastern side of Lake Ymandra. Nevertheless, the winds are exceedingly strong and penetrating, reminding one of a mid-Atlantic gale. Khibiny is north of the Arctic Circle, in lat. about $67^{\circ} 44'$. The station is chiefly devoted to the breeding of vegetables suitable for this northern climate. Many varieties of potatoes are being tested, also beets, sugar beets, radishes, and other

vegetables. Huge strawberries are grown successfully. Oats are successful for fodder, but will not ripen in the short season. Such plants as flax, hemp and Ricinus were also being tried. Even cotton and maize were being tested and their reactions noted. The maize was only two inches high, while the cotton, having reached a considerable height, promptly died.

The Plant Breeding Station was begun in 1923, as a part of the Government's scheme for colonisation ("Canadisation") of this region from the south. The trees had first to be felled and the ground cleared of mosses before anything could be planted. Now several acres are in cultivation with oats, vegetables, and other crops. The Laboratory, a log house with four rooms on the ground floor, was built on an eminence overlooking Lake Ymandra. Beside it is a cellar covered with turf, for storage of vegetables in winter. A larger building is being built outside the stockade.

A colony of new log cabins has been built near here, and the older part of the village stretches farther north along the Lake. The colonists get a grant of 2,000 roubles (£200) each from the Government, 1500 of which must be paid back without interest in ten years. They are given a piece of land on which they build a log cabin. This can also be inherited by their descendants, but if the land is not developed it reverts to the State.

In Soviet Russia, north of Lake Onega, the Government has established seven large colonisation areas, the three largest areas being in Murmansk itself. Here primitive log huts are being built as colonists come northwards. The older Russian houses are similarly constructed of logs below, but are characteristically ornamented with sawn wooden trimmings. The railway station at Medvezhya Gora, at the northern end of the beautiful Lake Onega, is very artistically ornamented in this way.

Although the summer season is very short, the temperature at the end of August was warmer than I anticipated. This is because the Behrens Sea and Kola fiord are warmed by the Gulf Stream. The snow in winter does not exceed 1.5 m. in depth and the rainfall is about 450 mm.; remnants of snow were still visible in some of the depressions on the higher mountains. The mid-temperature in February is -13°C ., the lowest recorded temperature being -38°C . Summer begins in the middle of June, when the ice goes out of the Lake, and lasts until nearly the end of August, hence about ten or eleven weeks. The last frosts occur about June 10th-15th and June is the warmest month, its mid-temperature being 12° - 15°C . and maximum 30°C . From May to August there is very little rain, the rainfall being so low that plants from Turkestan die here from drought. The season from August to October is, on the contrary, very rainy. The winds are very strong and they appear to be almost continuous, often reaching over 40 miles per hour. These heavy winds are an important element in the climatic conditions. During my week at Khibiny they were so strong that it was never safe to try and cross the lake in a motor boat. White caps which would have swamped it were always in evidence.

Snow begins in October, and by November the lake is frozen. At the time of my visit in the end of August, the period of continuous day was past, but the night was very brief and it was already light at 2.45 a.m. The aurora borealis begins about the middle of August and is very bright on clear cold nights. During the summer there are millions of mosquitoes, but at the end of August only a few remain. The whole flora of this region is supposed to number not more than three or four hundred species of flowering plants.

On the eastern side of the lake is a range of hills, the Khibiny mountains, which reach a height of nearly 4000 ft. On the morning after my arrival we set out to climb one of the nearer peaks, which was over 1500 ft. high, and had a small meteorological station at the top. This was the occasion for some interesting observations of the flora and geology of the region. Lake Ymandra was formerly much larger than now. It empties into the White Sea by the River Niva at Kandalaksha. In beginning the ascent, earlier shore line levels could be clearly traced on the slopes. The lower levels are composed wholly of morainic material full of boulders in glacial till. This material has evidently been cut into and shifted by streams many times in the post-glacial period. Some of it is nearly bare of vegetation, except scattered trees which have been killed by fire.

On the lower slopes we find *Pinus sylvestris* var. *lapponica* and *Picea obovata* Ledeb. (the eastern form of *P. excelsa*), with small birches, *Betula pubescens* and *B. verrucosa*. These are the only trees in the Kola Peninsula. *Betula nana* is also found on these moors but becomes commoner as we ascend the mountain. It occurs amongst a characteristic undergrowth containing an abundance of *Vaccinium uliginosum*, *V. myrtillus* and *V. vitis-idaea* as well as *Arctostaphylos uva-ursi* together with *Rubus saxatilis*, *Ledum palustre*, *Epilobium angustifolium* and *Deschampsia flexuosa*. *Calluna vulgaris* was common but not very abundant. The *Vacciniums* were covered with an abundance of blue berries, each species having its own flavour and range of shape¹ and size, but slightly bitterish at first, and none perhaps so tasty as the Canadian blueberry, *V. pennsylvanicum*. But they were sufficiently attractive so that we were continually stopping to pick and devour a few handfuls. Women come and collect them in quantities. Other plants which give character to these slopes are the mosses: *Hylocomium splendens*, which forms large soft springy masses, and *Hypnum Schreberi*, as well as *Polytrichum commune* and *P. stricta*. Ground lichens were here, such as *Cladonia alpestris* and *C. rangiferina*, but not in conspicuous quantities.

Climbing to the second former lake level, the slopes have scattered trees, mostly *Pinus* with some *Picea*, and the ground between is covered with *V. myrtillus* mingled with some *V. uliginosum*.

The third level is 100 m. above the lake and 230 m. above sea-level. Here

¹ I observed a variety of *V. uliginosum* with quadrate fruits, another variety with pear-shaped, and a third with elongated cylindrical fruits.



Phot. 2. Rock pool above the tree limit (Khibiny Mountains). Dwarf *Salix* and *Eriophorum vaginatum*.



Phot. 4. *Pinus sylvestris* var. *lapponica* and *Abies incana* at the mouth of the river Lunarnaioki near Khibiny.



Phot. 1. Mountain forest of *Picea* and *Pinus*, near tree limit (Khibiny). Ground vegetation of *Lactinium*, *Empetrum* and *Hylcoenium*. Note the dead branches and tops of the trees of *Picea*.



Phot. 3. View from summit, 500 m., showing stony slope in foreground, tree limit and Lake Vmandra.

is alpine forest of rather scattered smallish trees, nearly all *Picea obovata*, but a few birches (*B. pubescens*) and pines. The *Picea* is now covered with lichens, the most abundant being the blackish *Alectoria jubata*, but often intermingled with it is *Usnea barbata*; and *Evernia prunastri* is also common. The open spaces between the scattered spruces are covered with *Vacciniums* and a very little *Empetrum nigrum*. The latter becomes more abundant and more reduced at higher levels (Phot. 1). *Hylocomium* is in great masses and the *Vacciniums* grow amongst it. The *Cladonias* are now commoner. The spruce here has an interesting habit which I have not seen recorded elsewhere. The trees form masses of branches from their roots, but only on the side of the tree facing towards the south. This interesting habit gives a peculiar appearance to the basal part of the tree, with branched outgrowths on one side (Phot. 1). *Arctostaphylos alpinum* comes in here and quite replaces *A. uva-ursi* on the higher slopes. Small birches continue, and *Ledum palustre* becomes less common. *Juniperus communis* is present and *Linnaea borealis* near the end of its flowering season with almost white flowers. *Geranium pratense* with large bluish flowers and small *Sorbus aucuparia*, a few feet high, were also seen, as well as the oak fern (*Phegopteris dryopteris*).

Ascending further, we pass the edge of the tree line. The rocks are of nepheline syenite cleaved and faulted into large squarish masses only partly covered with vegetation. Here is *Loiseleuria procumbens*. In pools caused by the faulting of the rocks are beautiful colonies of *Eriophorum vaginatum* and *E. polystachyon* (Phot. 2). Dwarf willows of various species grow by these pools, and such plants as *Taraxacum* sp., *Pinguicula vulgaris* and *P. alpina*. Blue-green algae flourish in the fringing mud, and some of the pools of clear water contain great brownish masses of diatoms. Several ferns luxuriate in deep sheltered clefts in the rocks. These slopes above the tree line are exposed to continual heavy winds, and in places the stones are more or less bare ("Fjældmark") owing to heavy weathering. *Betula nana* now becomes common and small birches (*B. pubescens*) are found two or three feet high. The cold winds inhibit tree growth; but spruces and junipers continue nearly to the top as creeping Krummholz, growing always towards the leeward, and often hanging down in characteristic masses over the rocks, which are frequently in the form of gigantic steps, with crevices several feet deep between them. *Vaccinium uliginosum* continues, but reduced in size; *Tofieldia alpina* is common (*T. borealis* being found at low levels near the lake). The mosses are less deep and the lichens more abundant, forming masses over the rocks on these bare, wind-swept slopes. *Ledum palustre* is still found but is no longer common.

The most typical plants at this altitude are *Arctostaphylos alpinus*, *Cladonias*, *Betula nana*, mats of reduced *Vaccinium* and *Andromeda polifolia*. Other characteristic plants are *Juniperus nana*, *Antennaria dioica* and certain species of *Carex*. This is typical rock tundra.

Over 20 species of *Carices* occur in this region and several are characteristic

of the highest levels. They often form large yellowish patches on the hills, which can be recognised at a distance. It would be an interesting study to work out the details of their local altitudinal distribution. *Godetia alpina* was found here in seed.

Still higher on the rocky exposed slopes we find *Picea*, *Betula nana* and *Juniperus nana* as creepers, the last two becoming very common. *Silene acaulis* occurs at this altitude as well as by the lakeside. At the extreme top are *Linnaea borealis* (which I was surprised to find in such an exposed situation, as in Canada I have known it chiefly in the shade of deep woods among mosses), *Dryas octopetala* and *Juncus* sp. On the slopes just below the summit, lichens, chiefly *Cladonias*, become very common. They make a springy carpet covering the rocks and form the chief element of the vegetation. This is also typical rock tundra, but with a greater quantity of lichens. The last flowering plants to survive on the highest peaks are *Oxytropis campestris* and *Saxifraga oppositifolia*. Phot. 3 is a view overlooking Lake Ymandra from the top of our peak over 1500 ft. high.

I am told that, as one goes northward, the mountain top vegetation is found at lower and lower altitudes, until, on the Murmansk coast, it comes right down to sea level and covers the whole country, which is quite devoid of trees. From the account of Summerhayes and Elton (1923), it is clear that similar conditions prevail in Spitsbergen, but with a still greater paucity of plants, especially Phanerogams.

On our way down the mountain, having reached quite a low level, I happened to find *Cotoneaster uniflorus*, which is recorded from this region in *Flora fennica*. It is a low shrub (6 ft.?) with berries like *Sorbus aucuparia* but larger and pale reddish yellow, occurring singly; leaves entire, petiolate, nearly orbicular. I was a little surprised also to get *Orchis maculata* on this expedition, its pale purple flowers having darker markings, while the leaves had purple spots. *Selaginella selaginoides* Link. in quantity was another find. With the habit of a small *Lycopodium selago* and the lower sporophylls bearing each a megasporangium with four huge megaspores, like eggs in a basket, as well as having a ligule in the axil of every leaf, it combines the main features of the genera *Lycopodium* and *Selaginella*, showing that they must really be very closely related and indicating that heterospory must have been rather quickly attained from homospority in evolution.

On the following day, August 28th, we studied the vegetation along the shores of Lake Ymandra. On the sandy beach are scattered polsters of *Silene acaulis*, *Papaver radicatum* var. *lapponicum* with large yellow flowers, *Saxifraga aizoides*, *Empetrum nigrum*, *Calluna vulgaris*, *Oxytropis campestris*, *Arctostaphylos uva-ursi*, with wide stretches of bare sand between. These species show a striking root development. A remarkable and surprising feature is that they all flower twice in the short season, first in June and again in August. Many were now in full bloom.

Calypso borealis was also found here. *Alnus incana* is common, occurring in clumps about six feet high, and serving as a protection for *Empetrum*, *Calluna*, *Salix alba* and *Vaccinium uliginosum*, which form a covering on the ground under and between the alders.

Immediately behind the beach the sand is almost completely covered with these creeping plants growing amongst scattered pines, spruces, and alders. The river Lutnarmajoki flows into the lake here, forming a small delta and channels in the sand. The cliff at this point bears a characteristic grove of pines (Phot. 4), among which is a Lapp graveyard. By the beach were a number of dried up pools in the bare sand. Around the edge of some at a certain level was a complete ring of *Saxifraga aizoides*, as though the seeds had floated there and germinated simultaneously as the pools were drying up. Frequently no other plants were found in these shallow pool areas.

Along the banks of the river, which at this season is low, we found *Oxytropis*, *Saxifraga oppositifolia*, *Papaver*, *Alnus*, *Salix*, etc. In the turf along the riverside were such mesophytes as *Heracleum*, *Alchemilla vulgaris*, *Tussilago farfara*, which is small but common, and also *Godetia alpina* and *Polygonum bistorta*. Higher up the river we reached steeper slopes and the river became rapid. It is still working over the morainic material, and in spring is a roaring flood. In some places one bank is mostly till and is rapidly eaten away, while the other is full of boulders.

At several places we came upon groups of young birches about 15 feet high, which had been cut about two feet above ground so that they fell over without being completely detached. The small branches with the leaves attached are then cut off and dried in the sun to make "wild hay" or "tree hay." The same is done with willow and to some extent with alder, but the latter is not so good because it contains astringent tannin. In birch hay the leaves remain green but in the alder they go brown. In winter they are fed to the sheep, which eat them, branches and all, but for cows the leaves are stripped off and mixed with hot water and rye meal.

Higher up the river was a large birch-alder community with *Salix alba* about 15 feet high. *Salix* thickets as high as a man are recorded in Greenland from lat. 68° N. In lat. 73° N. these were only two feet high (Schimper, p. 688). Behind this is *Picea* with occasionally *Pinus*. We are now entering the valley between two hills which give protection from the winds. As the valley floor rises the woods become dense. They are chiefly alder, with spruce, willow and birch. In the undergrowth was *Maianthemum bifolium*, *Geum rivale* (tall), *Heracleum* sp., *Marchantia*, *Epilobium* sp., *Geranium* sp., *Calamagrostis*, *Trollius europaeus*, *Sorbus aucuparia* only two feet high, *Tussilago farfara*, *Equisetum sylvaticum*, *Prunus padus*, *Melampyrum* sp. and *Trientalis europaeus*.

Ascending the valley, we gradually entered an old primeval alpine forest, mostly of *Picea*. The ground is heavily carpeted with *Vaccinium*, chiefly *V. myrtillus*. Higher up, this partly gives place to *Empetrum*. This forest has

never been disturbed by man or burnt. It contains many old fallen logs, rotting and covered with mosses and lichens (see Phot. 1).

The valley now ascends rapidly. *Betula nana* comes into the heavy carpet, which is chiefly composed of masses of *Hylocomium* and *Sphagnum* with only a little *Cladonia* and other lichens. Among the moss grows a large and luxuriant *Umbilicaria*, but the forest has essentially a moss bottom and not a lichen bottom. Pine becomes commoner, replacing spruce as we ascend the valley. But the relative frequency of these two conifers depends much upon a northern or southern exposure. *Juniperus communis* grows among the moss in this typical alpine forest. Alternating with the mosses are hillocks of *Vaccinium myrtillus*, *V. vitis-idaea* and *Empetrum nigrum*, with a few stray stalks of *Deschampsia flexuosa*.

Linnaea borealis in the woods has a corolla which is white outside but with pink markings inside. On the exposed lake shore it is now out of flower but is said to be rose-coloured. In Canada, where it grows in deep woods among mosses, its dainty bells are typically pink within and without.

Other plants we encountered near the lake were *Parnassia palustris*, not uncommon and *Eriophorum alpinum*, an interesting species only four to six inches high, with few plumes and a long slender rhizome sending up shoots at very short intervals. *Allium schoenoprasum* with red flowers grows here, as well as *Silene inflata*, *Ulmaria palustris*, *Comarum palustris*, *Rosa acicularis*, *Prunus padus* and *Lonicera coerulea*. Dr Hurst informs me that this is the farthest north yet known for *Rosa acicularis*, the previous most northerly record being in Alaska.

One generally thinks of tundra as a vegetation composed of lichens and mosses growing on a soil which is only thawed to a certain depth during the short summer in Arctic latitudes. But tundra vegetation is by no means confined to level plains. There are, however, various kinds of tundra in different parts of Russia, and at different altitudes. Schimper (1903, p. 685) distinguishes moss tundra and lichen tundra, the former on dryer soil. He also recognises *Cladonia*-tundra, *Platysma*-tundra (with *Cetraria*, etc.) and *Alectoris*-heath.

A first division would be into (1) rock tundra, and (2) moor tundra. The former occurs under more rigorous conditions, at higher altitudes or latitudes, where there are bare patches on a stony soil. The dwarf-shrub tundra of Central and Southern Greenland, with evergreen shrubs such as *Empetrum nigrum* and *Cassiope tetragona*, six inches high mingled with mosses and lichens, clearly resembles in general character some of the Khibiny tundra.

We may now attempt to classify further some of the main types of tundra vegetation.

(a) Rock tundra is found along the Arctic coast at low altitudes down to sea level. It is very similar to and contains the same species as the (b) mountain rock tundra already described in the mountains above the tree line. Moor



Phot. 6. This forest of *Pinus* with *Chionitis* ground vegetation, near eastern shore of Lake Ymandra. (Photograph by Dr Eichfeld.)



Phot. 8. "Lake of Stones" in low Tundra. Polygonal areas of bare soil forced up by frost between the stones. *Carex* and *aquatic* the only flowering plant. Background as in Phot. 6.



Phot. 5. River Lutnarmajoki flowing over moraine country. This forest is of *Picea*, *Pinus*, *Betula* and *Salix alba* 15 feet high.



Phot. 7. "China" tundra, west of Lake Ymandra. (Photograph by Dr Eichfeld.)

GATES—NOTES ON THE TUNDRA OF RUSSIAN LAPLAND

tundra is typical of Siberia. There is very little of it in the Kola Peninsula. It occurs on low level ground.

Phot. 6 shows typical *Cladonia* moor tundra with *Pinus*, occurring near Lake Ymandra. *Cladonia rangiferina*, *C. alpestris* and several other species of *Cladonia* cover the ground, giving a whitish appearance to the landscape. Reindeer feed on it in winter by pawing away the snow. *Umbilicaria* and other lichens grow here as well as *Empetrum nigrum*, *Arctostaphylos uva-ursi*, and *Calluna vulgaris*. What is called *chuna* tundra occurs on open moor slopes and consists of ground lichens intermingled with masses of reduced, creeping shrubs (Phot. 7).

Another type (c) of tundra, which occurs in the Ural Mountains, is known as "Fleckentundra" (patchy tundra). It does not occur in the Kola Peninsula. It is characterised by its patchy covering of vegetation with areas of bare yellow clay between. I shall refer to it again later. The last type (d) of tundra, which I was told occurred in the Kola Peninsula, but which I did not see, is called in Russian *Klochkovataya* or Tufted Tundra. The plant species are the same but the surface of the ground is broken into more or less polygonal areas, with deep crevices between them. This is evidently a form of rock tundra. The crevices may be as much as ten feet deep and six feet wide, while the Klotshky or higher areas may be 30 ft. wide and are covered with vegetation, as are also the bottoms of the crevices. This formation appears to resemble the limestone pavement with crevices in Northern Lancashire, visited during the Liverpool meeting of the British Association, except that here only the crevices bear vegetation.

Interesting in connection with the Fleckentundra was a "lake of stones" covering several acres, part of which is shown in Phot. 8. This was a low area flooded in winter and spring when the snows melt, but now a level surface of bare stones (diabase?). In small pools between the stones were colonies of several blue-green algae; but the whole area was otherwise devoid of plants, except a line of *Carex aquatilis* growing inwards from the margin in places (see Phot. 8). The significant feature is that here and there between the stones are patches (Flecken) where the soil has been forced up between the rocks by the frost, through expansion of the wet soil in freezing. This soil remains entirely bare of plants, no doubt owing to the continued action of the frost.

This formation appears to resemble Fleckentundra in certain respects, but in the latter the spaces occupied by bare clay are much larger, while instead of bare stones there is a turf of tundra plants. Probably moor tundra would become Fleckentundra in a soil containing glacial boulders if there were greater frost action in the wetter parts of the soil. Huxley and Odell (1924) have described stone polygons and other results of frost action in Spitsbergen, but this particular condition does not appear to have been observed.

In returning southwards from Khibiny by train, one noticed a gradual but

marked increase in the luxuriance and extent of the forests (mostly *Pinus sylvestris* var. *lapponica*) before reaching Kandalaksha (lat. 67° 10' N.). The real tundra appears to begin north of this point and well within the Arctic circle. I was interested in the question of the relation between *Pinus sylvestris* and its var. *lapponica*. The latter differs in being more stunted and in having shorter and fewer needles, and the condition becomes more marked as one goes northwards; but *lapponica* appears to be not merely a growth form, for both the species and its variety occur nearly as far south as Moscow, sometimes intermingled under apparently the same conditions. Intermediate forms, which may be hybrids, also occur.

South of Kandalaksha hayfields first begin to appear, but they are very few and the country is mostly wooded or barren and swampy. At about 64° N. spruce becomes the dominant element of the forests, while the pine continues. *Cladonia* has nearly disappeared from the ground, which is covered by *Calluna*, together with *Polytrichum*. *Epilobium* is common, and small birches where the conifers have been cut. The temperature is already markedly warmer.

Southwards along Lake Onega are forests of pine, spruce and birches, less stunted than in the north, together with a few *Populus tremula*, which becomes more common to the south. *Sorbus aucuparia* is common and much larger than in Murmansk; *Epilobium angustifolium* occurs in masses. Farther south some of the woods are almost entirely birch. *Phragmites communis* probably occurs commonly on Lake Onega, although I first saw it somewhat further south.

The animals of the Murmansk region show some interesting inter-relationships. The number of reindeer is estimated at 13,000. They are semi-domesticated, but the Lapps frequently lose them because they wander northwards in search of lemmings which they eat with great avidity. They are by no means the only herbivorous animal which develops a liking for a flesh diet in these northern latitudes. The Lapps keep cows as well as reindeer, and the former, in addition to their "tree hay," are fed on fish entrails which are collected for the winter and mixed with the leaves. The mixture reeks horribly but the cows like it. I am told that it is impossible to remain near while it is being fed to the cows, and the milk tastes of it. On the Murmansk coast the cows also eat seal meat and drink fish oil. The sheep eat the carcasses of seals (*Phoca*) left on the shore after the skin is removed. They devour them like dogs, eating the bones and leaving nothing behind.

Bear meat is frequently eaten in the Khibiny region, and the Lapps eat it raw. They also feed on what is called "sour fish," i.e. fish which has been caught and put in a sort of silo. When ready to be eaten, the fish are rotten and smell horribly. Another habit of the Lapps is to castrate the reindeer, when about 1½ years old, with their teeth. They insist that this method is better than the use of a knife, as a portion of the testis is left and hæmorrhage is prevented. It is possible that this custom is a survival from Neolithic times before iron

was available, but I am informed that similar methods are used with lambs by the shepherds in parts of Wales.

Dr Eichfeld finds great variation in the frequency of animals in this region from year to year. An abundance of birds depends upon abundance of fruits and berries. Following the birds, the shrews (*Sorex vulgaris* and *S. pygmaeus*) become numerous, then the lemmings, then the foxes (the Arctic as well as the red species) which feed on lemmings. The bears eat the foxes and are very abundant in some years. Hence one cycle depends upon another. The animals seem to occur abundantly in cycles of five to seven years, migrating across the country from N.E. to W. by S. The squirrels (*Sciurus vulgaris*) have an independent cycle of about seven years, which depends upon the abundance of cones of *Picea* and *Pinus*. In some years the squirrels become extremely abundant, but I did not hear or see a single one.

This varying abundance of species is an important factor in animal evolution, as Elton (1924) has pointed out, and appears to be particularly characteristic of the high northern latitudes. Elton finds that the periodic fluctuations in lemmings have an average period of about $3\frac{1}{2}$ years, the maximum numbers occurring synchronously in North America and Europe. The varying hare (*Lepus americanus*) in Canada has a period of 10 or 11 years. Elton points out that the sunspot cycle of 11 years appears to agree with the evidence of climatic cycles derived from lake-levels and the thickness of the annual growth-rings in trees. It also agrees very well with the frequency cycle of some animals. For example, mouse plagues occur in Britain every 11 years, at the time of the sunspot minimum, though sometimes a period is skipped. There is need for much further study of this subject, and it can best be done with Arctic animals and plants.

A partial list of plants from the Khibiny district, the mountains and the Kola peninsula was published by G. N. Anoofriev in *Geog. Inst.* 1922. The following list, containing my own observations, is based upon that, but contains a number of additional species. Those in the list which I did not see are enclosed in parentheses. I am indebted to Miss Lorrain Smith for identification of the lichens.

LICHENS.

| | | |
|----------------------------------|----------------------------------|-----------------------------------|
| <i>Umbilicaria</i> sp. | <i>C. deformis</i> Hoffm. | <i>A. ochroleuca</i> Nyl. |
| <i>Cetraria islandica</i> Ach. | <i>C. gracilis</i> Willd. | <i>A. cincinnata</i> Nyl. |
| (<i>C. hians</i> Th. Fr.) | (<i>C. uncialis</i> Web.) | <i>Evernia prunastri</i> Ach. |
| (<i>C. nivalis</i> Ach.) | (<i>C. alpestris</i> Rabenh.) | <i>E. divaricata</i> Ach. |
| <i>Cladonia rangiferina</i> Web. | <i>C. coccifera</i> Willd., etc. | <i>Parmelia</i> sp. |
| <i>C. sylvatica</i> Hoffm. | <i>Usnea barbata</i> Fr. | <i>Lecladophila cricetorum</i> A. |
| <i>C. crispata</i> Nyl. | <i>Alectoria jubata</i> Nyl. | Zahlbr. |

BRYOPHYTES.

| | | |
|-----------------------------------|-----------------------------------|---------------------------------|
| <i>Cephalozia</i> sp. | (<i>S. compactum</i> De.) | <i>Hylocomium proliferum</i> L. |
| <i>Marchantia</i> sp. | (<i>S. warnstorffii</i>), etc. | <i>H. splendens</i> Hedw. |
| <i>Sphagnum acutifolium</i> Ehrh. | <i>Polytrichum strictum</i> Banks | <i>Hypnum schreberi</i> Willd. |
| (<i>S. fuscum</i> Klingg.) | <i>P. commune</i> L. | (<i>H. fluitans</i> L.) |

PTERIDOPHYTES.

Equisetum limosum L.
(*E. palustre* L.)
E. sylvaticum L.
(*E. variegatum* Schleich)

Lycopodium annotinum L.
L. alpinum L.
L. selago L.
L. complanatum L.

L. clavatum L.
L. lapponicum
Selaginella selaginoides Link.

CONIFERS.

Pinus sylvestris L. var. *lapponica* Fr.

Picea obovata Ledeb.
Juniperus communis L.

J. nana Willd.

MONOCOTYLEDONS.

(*Sparganium* sp.)
(*Agrostis canina* L.)
A. alpina Scop.
Calamagrostis, 2 spp.
Deschampsia flexuosa (L.), Beauv.
Festuca rubra Hack.
Molinia coerulea Moench.

Melica nutans L.
Poa alpina L.
Phleum alpinum L.
Eriophorum alpinum L.
E. vaginatum L.
E. polystachyon L.
Scirpus caespitosus L.
Carex, over 20 spp.

Juncus alpinus Vill
(*J. biglumis* Linn.)
Tofieldia borealis Wahlenb.
T. alpina Sm.
Maianthemum bifolium Salisb.
Paris quadrifolia L.
Orchis maculata L.
Calypso borealis (L.) Salisb.

DICOTYLEDONS.

Salix herbacea L.
(*S. glauca* L.)
(*S. lanata* L.)
(*S. lapponica* L.)
(*S. myrsinites* L.)
(*S. reticulata* L.)
S. alba L.
Betula pubescens Ehrh.
B. verrucosa Ehrh.
B. nana L.
(*B. kusmischeffii* (Regel) Gürke)
Alnus incana Willd.
Rumex acetosella L.
Polygonum viviparum L.
P. bistorta L.
Silene acaulis L.
(*Gypsophila fastigiata* L.)
Stellaria palustre
Trollius europaeus L.
Thalictrum sp.
Papaver radiculatum var. *lapponicum*
Drosera anglica Huds.
(*D. rotundifolia* L.)
Saxifraga aizoides L.
S. oppositifolia L.
S. stellaris L.
Parnassia palustris L.
Dryas octopetala L.
(*Cotoneaster vulgaris* Lindl.)

C. uniflorus Bunge
Sorbus aucuparia L.
Rubus chamaemorus L.
(*R. arcticus* L.)
R. saxatilis L.
Potentilla norvegica L.
(*P. tormentilla* Neck.)
(*P. intermedia* L.)
P. palustris (L.) Scop.
Rosa acicularis Lindl.
Geum rivale L.
Prunus padus L.
Ulmaria palustris
Astragalus alpinus L.
Oxytropis lapponica Gaud.
O. campestris DC.
Geranium pratense L.
Empetrum nigrum L.
Epilobium angustifolium L.
E. palustre L.
E. collinum Gmel.
Godetia alpina
Hieracium sp.
Cornus suecica L.
Pirola secunda L.
P. uniflora L.
Ledum palustre L.
Cassiope hypnoides D. Don.
C. tetragona D. Don.
Loiseleuria procumbens (L.) Desv.

Andromeda polifolia Spr.
Arctostaphylos uva-ursi Spr.
A. alpina Spr.
Vaccinium myrtillus L.
V. vitis-idaea L.
V. uliginosum L.
Oxycoccus palustris Pers.
O. microcarpus Turcz.
Calluna vulgaris Salisb.
Phyllodoce coerulea (L.) Bab.
Diapensia lapponica L.
Trientalis europaea L.
Menyanthes trifoliata L.
Brunella vulgaris L.
Melampyrum pratense L.
Bartsia alpina L.
Pinguicula alpina L.
P. vulgaris L.
Galium palustre L.
Linnæa borealis L.
Lonicera coerulea L.
Campanula rotundifolia L.
Tussilago farfara L.
Carduus heterophyllus L.
Hieracium alpinum L.
Taraxacum sp.
Antennaria dioica Gaertn.
Achillea millefolium L.
Saussurea alpina DC.
Solidago virgaurea L.

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A PROPOSED BIOLOGICAL FLORA OF BRITAIN

By E. J. SALISBURY

IN the preface to the first edition of the *Student's Flora* published in 1870 Sir Joseph Hooker expressed the hope of being able to undertake a "companion volume" in which "the physiological and morphological observations" on British species should be recorded. Ever since that time this idea has been in the minds of botanists but, apart from unpublished notes respecting certain species prepared by the late Sir I. Bayley Balfour, no serious attempt has been made to bring the project to fruition. Such autecological data are of great value for their own sake, and the progress of the study of plant communities is greatly hampered by the lack of information respecting the life-histories and biotic relations of their constituent species. Further, until such data are available it is useless to attempt to unravel the complex tangle of factors involved in the phenomena of competition.

The Council of the British Ecological Society has had the matter under consideration and at the Annual Meeting held on January 7th, the Society decided to publish a British Biological Flora which should embody such data respecting the biology of the native and naturalised British species as have a bearing on their ecological relations.

The writer, who has been making observations and collecting data of this character with reference to British woodland species for some years past, has undertaken the preparation and editing of the work, but it is manifestly a task that can only be successfully accomplished by the active co-operation of botanists, both professional and amateur, throughout the country.

Much relevant information is to be found scattered through the multitude of botanical journals but is difficult of access. A great deal is also known to field-naturalists but has never been published, and is likely to be lost with the death of the individuals. It is proposed to incorporate in the Flora all accessible published observations together with the not inconsiderable mass of unpublished data. It is felt that such a compilation will be of great scientific value and at the same time provide the surest means of bringing to the notice of students the many lacunae that require to be filled.

The accompanying schedule, which has been prepared by the writer, is intended to indicate the scope of the projected work and the nature of the data required, but the plan is naturally subject to modification as need arises, and any suggestions or criticisms will be welcomed. Those possessing original observations suitable for incorporation are asked to communicate with the writer at Willow Pool, Radlett, Herts.

PROPOSED SCHEME FOR BIOLOGICAL FLORA OF BRITAIN
(PREPARED BY E.J.S.)

- A. Name of species with synonymy: varieties and ecads.
- B. Distribution (British, extra-British). Altitudinal range.
- C. Fossil and sub-fossil records.
- D. Soils: type, water content, reaction, carbonate content, organic content.
- E. Climatic conditions: rainfall range, light demands.
- F. Habitats, communities, status (abundance, frequency, constancy, exclusiveness, etc.).
- G. Biological type: perennial, biennial, winter or summer annual; mode of perennation; assimilation type; evergreen, summergreen, prevernal, etc.
- H. Phenology: first leaf, first flower, full flowering period, seed ripens, leaf-fall.
- I. Root system: type, volume occupied, average rooting depth, special features (e.g. adventitious shoots, distribution of root hairs, root nodules, etc.: in the case of geophytes the depth of the rhizome or bulb, etc., presence of contractile roots, etc.).
- J. Shoot system:
 - Average height of the vegetative organs. Leaf positions.
 - Hydathodes or extrafloral nectaries. Morphological transpiration checks or other features affecting transpiration.
 - Special anatomical features (aerenchyma, any special features of the chlorenchyma).
- K. Reproduction (sexual and asexual).
 - Fertility; whether self or cross-pollinated, whether self-sterile or self-fertile, or apogamous.
 - Pollinating mechanism: type of pollinating agent (if entomophilous the type only of pollinating insect, unless the latter is specially restricted to particular species).
 - Any special features regarding fertilisation (e.g. chalazogamy).
 - Seed output of normal plant (in the case of trees frequency of mast years).
 - Size and weight of seed.
 - Means of seed dispersal (or fruit dispersal).
 - Percentage germination. Duration of viability.
 - Period of germination in nature.
- L. Reproduction (vegetative).
 - Means of vegetative propagation. Rate of vegetative spread.
- M. Physiological features:
 - Sleep movements or other special responses as movements of flower and fruit stalks.
 - Osmotic pressure or suction force when known and observed range.
 - Special modes of nutrition (e.g. Mycorrhiza).
- N. Parasites (only when of especial interest, or very common, or where confined to a particular species and of general interest).
- O. Hardiness and susceptibility to destruction (by fires, animals, etc.).

REVIEWS

Elton, Charles. *Animal Ecology*. Pp. xx + 207, with 8 photographic plates and 13 diagrams in the text. $8\frac{1}{2} \times 5\frac{1}{2}$ in. London, Sidgwick and Jackson, Ltd., 44 Museum Street, W.C. 1. Price 10s. 6d. 1927.

We welcome most cordially this first English book (there are several American books) on *Animal Ecology* written by one of the keenest and most successful of our still very small band of animal ecologists. The subject has lagged seriously behind plant ecology for obvious reasons. It is very much easier to distinguish and describe communities of plants than communities of animals, and animal communities depend as a rule so closely on the plants that it is impossible to make very much headway with what may be called the systematic side of the subject until the plant communities are fairly well known and the laws of their succession understood. Another reason why "scientific ecology," as Mr Elton says (p. 3), "was first started some thirty years ago by botanists" is that "there are fewer species of plants than of animals" and "plants do not rush away when you try to collect them." The author's statement of the reasons for the neglect of animal ecology is that "the discoveries of Charles Darwin...gave a tremendous impetus to the study of species and the classification of animals...previous descriptions of species were too rough and ready...a revision and re-organisation of the whole subject was necessary....Half the zoological world thereupon drifted into museums and spent the next fifty years doing the work of description and classification which was to lay the foundations of the scientific ecology of the twentieth century. The rest of the zoologists retired into laboratories...." "The discoveries of Darwin, himself a magnificent field naturalist, had the remarkable effect of sending the whole zoological world flocking indoors...whence they are now beginning to put forth cautious heads again into the open air. But the open air feels very cold...and it is rather a disconcerting and disturbing experience to go out of doors and study animals in their natural conditions."

Botanists (or a few of them) having come into the open air again sooner than the zoologists, and having the advantage of less bewilderingly varied and less distractingly mobile objects of study, have accordingly laid the foundations of the systematic study of plant communities, while "animal ecologists," coming a little later, "have followed the lead of plant ecologists and copied most of their methods, without inventing many new ones of their own." It is one of the objects of Mr Elton's book to show that this is largely a mistake, "and that zoologists require quite special methods of their own in order to cope properly with the problems that face them in animal ecology." Here we may add that the animal ecologists seem likely now to have a little revenge, for the very fact that the delimitation and description of plant communities is easier and a good deal more advanced than that of animal communities tempts many plant ecologists (or shall we say plant sociologists?) in the direction of an easy and rather sterile formalism of description and analysis, and away from the more penetrating though more difficult and baffling study of the vital interrelations of plants with their conditions of life, while the zoologists are forced into this kind of study at once if they are to do anything at all beyond cataloguing species.

Mr Elton makes no effort to catalogue or even to indicate in outline all the known facts of animal ecology. After a series of introductory chapters in which he discusses Distribution of Animal Communities, Ecological Succession and Environmental Factors (showing that the distribution of an animal is determined by a few factors only which really limit its habitat and that it often possesses the *psychical* power of seeking its optimum environment,

thus avoiding the risk of running into dangerous conditions on the limits of its physiological tolerance), he finds four key principles in the light of which the baffling complexity of most animal communities may be successfully analysed. These are food-chains and the food-cycle, size of food, niches, and the pyramid of numbers.

The doctrine of *food-chains* simply means that the primary links in a community of animals and plants are those connecting the different groups of organisms with their appropriate food, in broad outline the carnivores with the herbivores on which they prey, the herbivores with the plants. The totality of the individual food-chains in a community is the "food-cycle." Food-cycles illustrated by diagrams are that connecting North Sea herring of different ages with the phytoplankton (Hardy), and the food-cycle of Bear Island in the Arctic with Bacteria at one end and the Polar Bear at the other (from the paper by Summerhayes and Elton published in this JOURNAL in 1923). The links of the food-chain, especially in the case of carnivorous animals, are largely determined by *size*, because on the one hand, an animal cannot tackle prey *above* a certain size (this is modified of course in the case of animals hunting in packs, and also in other ways, as by fierceness, skill, poison and fear) and on the other it is impossible to satisfy its hunger on prey *below* a certain size (though we are told that foxes find it worth while to live entirely on mice in years when these are especially abundant). Between these extremes there is an *optimum* size of food which is the one usually eaten. "Each stage in an ordinary food-chain has the effect of making a smaller food into a larger one, and so making it available to a larger animal. But since there are upper and lower limits to the size of animals, a progressive food-chain cannot contain more than a certain number of links, and usually has less than five."

The term *niche* is applied to the specialised occupation of an animal, usually in the matter of feeding or being fed upon. "When an ecologist says 'there goes a badger' he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said 'there goes the vicar.'" "There is often an extraordinarily close parallelism between niches in widely separated communities....the Arctic fox subsists upon the eggs of guillemots, while in winter it relies partly on the remains of seals killed by polar bears. The spotted hyaena destroys large numbers of ostrich eggs and also lives on the remains of zebras killed by lions." A striking niche is that occupied by species which pick ticks off other animals—the African tick bird from the skin of ungulates, making its nest of the hair of its "host," starlings in England from sheep and deer, a Galapagos scarlet land crab from the skin of the great aquatic lizard.

The *pyramid of numbers* is the picturesque name Mr Elton gives to the fact that on the whole the smaller an animal the more numerous it is (because it reproduces more quickly) and the nearer the bottom of a food-chain. The larger carnivores come at the top, and their size is correlated with their fewness and with the fact that they tend to be much more wide ranging and less strictly confined to one habitat than herbivores. They have to travel to get enough food.

While carnivores are necessarily considerably larger than the animals on which they prey, parasites are considerably smaller, so that the size-progression of the food-chain goes the other way—the pyramid of numbers is inverted; and while carnivores live on capital (though they must leave enough to enable the capital to be replaced) parasites may be said to live on income. The carnivore adopts the method of the burglar, the parasite of the black-mailer. Nevertheless it is possible to trace a complete series between the two extremes, and it is a mistake to imagine that parasites are unique in exploiting the activities and food products of their hosts. In fact "the whole animal kingdom lives upon the spare energies of other species, or upon plants." The "moral obliquity" which Mr Elton objects to being fastened exclusively upon parasites is surely mainly due to the fact that the more *completely* a parasite is adapted to parasitic life the less its muscular energy becomes, because it does not have to travel about and seize its prey but remains attached to the body of its host, and this

leads to degeneration of motile organs (or, in plants, of the food-forming equipment). On the standard of man, naturally an active animal, this leads to physical (and moral) deterioration. A burglar is from one point of view as immoral as a blackmailer, no doubt, but he is not so much disliked and despised by the rest of humanity, because he shows more physical activity and physical courage, qualities necessary to the primitively "normal" individual of the species. "Virtue" is primitively courage and normality, rather than respect for other people's property. If we were primitively a race of parasites our moral standards would doubtless be very different.

The inclusion of parasites in food-cycles lengthens and complicates them considerably, because the size range is greatly increased—down to bacteria—and because of the extraordinary complexity of the life-histories of many parasites owing to their power of passing from one host to another, for instance from prey to carnivore. Several instances of such complex life-histories and their effect on the food-cycle are given. Nevertheless as *sources* of food, parasites are on the whole insignificant, though they cannot be entirely neglected.

The enormous importance of the effects of regular or fluctuating periodicity in the environment of animal communities is well brought out in a chapter on "Time and Animal Communities." Every "place community" is divisible into "time communities" the members of any one of which do not normally meet those of another. One of the best known and most striking examples is, of course, the day and night fauna of a tropical jungle, though exactly the same thing may be observed in an English wood in summer. Then there is the more fundamental effect of the change of season, most strongly developed in temperate regions. In the Arctic life is practically suspended all winter, and in the summer when it is warm enough for the plant and animal communities to be active they are exposed to the unusual condition of continuous illumination, so that the day and night effect is suspended altogether. Then there are the fluctuating periodicities of *weather* and even smaller ones, such as the drop of temperature caused by the passing of a cloud over the sun, which slows down or stops the activities of many animals, especially insects. The influence of periodic conditions on animal activity seems to be mainly effected by the change of temperature or of moisture.

Two most interesting chapters are devoted to the subject of animal numbers, on which Mr Elton himself has carried out valuable researches. After emphasising the enormous numbers of wild animals which still exist in the world, though those of several of the larger ones (e.g. zebras, bison, whales and walrus) have been greatly reduced, sometimes almost to extermination, within the last century or so, the author calls attention to the sudden increases in the numbers of particular species, generally relatively small species, because these alone are capable of really rapid reproduction, which give rise to the phenomena of "plagues" and "epidemics." But even large animals which produce only one or two offspring a year, or reproduce at even longer intervals, would increase enormously in course of time if natural checks were not in operation. These checks depend in the first place on the organisation of the food-chains to which the animal belongs. One animal increases at the expense of another till a balance is struck which holds roughly between all the animals (and plants) of a food-cycle in a state of nature, any undue increase of one species being, as it were, automatically checked by a corresponding increase of a carnivore or parasite.

Thus we arrive at the conception of an *optimum density of population* for each species. If it increases much beyond this it tends to eat out its food supply, and the individuals are weakened and run the risk of wholesale death. Thus the "enemies" of a species are actually useful to it *as a species*.

Animals at the end of a chain, such as the large carnivores, which have no carnivorous enemies, regulate their numbers in different ways, many of which are largely obscure, but among which the division of the available country into separate "territories," each occupied by a single pair, is a noteworthy method. Individuals unable to obtain a territory presumably

die unmated. The "territorial system" is best known among birds, especially the warblers, where it has been worked out by Eliot Howard, but it doubtless applies to the large carnivores and perhaps to many other animals as well.

Nevertheless, in spite of all these automatic mechanisms tending to preserve "the balance of nature," the numbers of a species do sometimes increase almost up to the theoretically possible reproduction rate. Various insects, mice, lemmings, and even so large an animal as the South African springbok may be taken as examples. These vast and sudden increases are spectacular and attract the attention of man by the vast amount of damage the hordes of animals do. But almost any animal about which we know enough is found to vary in numbers from year to year. Familiar examples are the common wasps, and certain species of butterflies are well known to be much more abundant in some summers, but the principle seems to be universal, and it is often known to have a definite periodicity. These fluctuations are attributed by Mr Elton to instability of environment, such as is expressed in various climatic cycles—temperature cycles, rainfall and snowfall cycles, many of which have been shown to be correlated with sunspot cycles. The extreme conditions thus occasionally produced may act in many indirect as well as direct ways, i.e. through their effect on the food or on the enemies of the species. Thus the great mortality among small birds caused in England by the very severe winter of 1916–17, from which they have only just recovered, probably worked through starvation rather than directly through the cold. But many of the observed fluctuations in numbers have not yet been explained at all.

Sometimes fluctuations of external conditions cause a great increase in the numbers of a species. The "lemming years" so well known in Norway are an example. These have been shown to synchronise with the lemming years of Canada and they are therefore probably due in both countries to some climatic cycle common to both hemispheres. All small rodents for which there are any relevant data, as Mr Elton has shown, exhibit periodic variations of the order of three or four years. After the great increase there comes an equally sudden diminution, which seems to be usually brought about by an epidemic disease. It is probably advantageous for a species to have this great power of increase, even if it is in fact usually terminated by wholesale destruction through an epidemic, because it gives a margin which prevents the numbers decreasing towards extermination point if the "balance" with other animals is not struck exactly right. The great rodent fluctuations have of course widespread effects on the numbers of animals which prey upon them, e.g. the Arctic fox in the case of lemmings, but such consequent increase in the carnivores is seldom effective in reducing the numbers of the prey, because the larger carnivore cannot increase quickly enough to keep pace with the small rodent.

Dispersal of an animal species is, according to Mr Elton, usually a slow, imperceptible process resulting directly from wandering in search of suitable food or a suitable breeding place. It is only sessile or comparatively sessile animals which have "dispersal mechanisms," such as plants have. And spectacular "migrations" of animals, of which the periodic migrations of birds are the best known examples, generally have nothing to do with the "dispersal" of the species, though in some cases they do result in its establishment in a new place. Many animals are of course "dispersed" by "accidental" means, i.e. with the help of the wind or of floating logs, on ships or attached to other animals, and this kind of travel, besides active migration, may result in the spread of the species, though a large majority of the migrants die after arrival owing to conditions being unsuitable or the failure to find suitable food or mates. Even if they survive for a time it by no means follows that the species becomes established in the new locality. The definitely directive force of some tropism or instinct may settle the animal in a suitable habitat after a long undirected journey. The author emphasises the fact that it is usually incidentally that relevant facts about the dispersal of particular animals are discovered, and hence the great importance of publishing all such observations, however fragmentary they may be.

In the chapter on "Methods" (which is, for the most part, equally valuable to the plant ecologist) the author points out that it is essential to *select* facts for observation and record. The notion that facts can be recorded by an observer unprejudiced by any theory is futile, and such records would be of little use if they were possible. The great thing is to be able to appreciate what facts are significant in relation to a given idea, though of course it is also true that facts constantly turn out to be useful from points of view other than those in the mind of the observer. Another important point is to make records as exact as possible, for example always to record the *species* of both eater and eaten, and, if the observer does not know it, to take the trouble to find out from a specialist. The great bulk of recorded observations are of much less use than they might be owing to the neglect of this principle, and such records are responsible for much of the lack of sympathy with ecology frequently met with on the part of systematic specialists. Such specialists feel too that ecologists, even when they do take the trouble to get the species they observe correctly named, are rather parasitic upon the labours of others. This is true, but it is not a thing to be ashamed of. In the present state of biological science nearly all workers are bound to be more or less parasitic—they must use the work of others on every hand. When the classification is to some extent settled, at least to the point of general agreement as to what is meant by a given name, the work of the taxonomic specialist will become more and more that of naming specimens for other people. It is important that the ecologist should know not only the chief published systematic descriptions of the various groups but also the names of specialists able and willing to name his species. He should also pay attention to the systematic collection (for which he has unique opportunity) of material, properly and carefully labelled, for the taxonomist, and in this way he can repay some of the debt he owes to the systematist, and help to reveal the existence of hitherto unknown forms, often differing perhaps in habitat, in behaviour, or in other characters which are not morphological. This chapter also contains a lot of valuable hints to animal ecologists about detailed methods of observation and common mistakes and omissions made by observers, and remarks about different ways of tackling the important problem of determining animal numbers.

In a chapter on "Ecology and Evolution" the author, after stating his belief that natural selection *must* be an important factor in evolution, calls attention to the existence of dimorphism in the colours of certain species, one colour harmonising with the theory of protective colouration, the other being in violent discord with it. He points out that practically all field naturalists of wide experience disbelieve in the general theory, and mentions also the conclusions of Richards and Robson who say that very closely allied species practically never differ in characters which by any stretch of the imagination can be called adaptive. This is too wide a statement for plants, but we can quite safely say that a vast number of closely allied species are not separated by adaptive characters. The author's conclusion is that genotypic variations *must* spread in a species by some means other than natural selection, that new varieties and species are established in this way, aided by various factors which lead to isolation, and that natural selection is ultimately effective, probably acting rather on populations than on individuals. With some such general statement it is difficult to disagree. The problem is to understand in detail in particular cases how the spread of the new genotypic variations is effected. Mr Elton suggests that the great fluctuations in animal numbers may provide a partial key to the solution. If new heritable variations arise in a population whose numbers are at a low ebb, so that the struggle for existence is partly suspended, then, when the great increase in numbers arrives, the new variation will automatically spread very quickly, and a very large proportion of the new large population will possess it. It is clear that ecological work alone can settle such questions, and is therefore essential as a contribution to any complete understanding of the mechanism of evolution.

It will be clear from the fairly full account that has been given of the nature of the

contents of Mr Elton's book that it is an original book, in some ways a pioneer book, and well worth the study of all ecologists. It is packed with interesting and significant facts, arranged not systematically in the ordinary sense but to illustrate the author's effort to find the most fruitful ways of studying the ecology of animals. Mr Elton has a singularly candid and open-minded way of looking at all his problems, which he discusses with a charmingly ingenuous humour.

We may now look forward with some confidence to a period of intimate co-operation between botanists and zoologists in ecological work, a period which we expect will be fruitful to a degree hardly yet suspected. The results which may be anticipated will be two-fold: first a really accurate knowledge of the nature and evolution of what the Americans call the "biota" of the world, based on a complete study of their composition, behaviour and history, and of the nature of the species which enter into them; and secondly the first really trustworthy body of knowledge which can be used in the solution of many of the great economic problems which face the modern human world.

Professor Julian Huxley contributes a notable Introduction in which he argues that the zoological course in a university should no longer consist mainly of comparative morphology with the other subjects which have developed in recent years "tacked or thrown on here and there like valances or frills or antimacassars." Even if morphology is the "backbone" of zoology, as is often urged by zoological teachers, "an animal whose backbone weighed more than its muscles, nervous system and viscera combined would be biologically very inefficient." It is not true that other zoological subjects can only be tackled successfully after the acquisition of a detailed and intensive knowledge of the morphology of the various groups of animals such as is usually required for a zoological degree, though a general survey of the main types of structure and development among animals is a desirable preliminary. Prof. Huxley suggests that there should be a series of courses of approximately equal "value," each covering one of the main fields of biological enquiry, of which he mentions ten: vertebrate morphology, vertebrate embryology, invertebrates and lower chordates, cytology and histology, genetics, developmental physiology, faunistic zoology and ecology, comparative physiology, animal behaviour, evolution. The difficulty about this sort of programme is for the head of a department to find the people able and willing to give such a series of courses. He has to subordinate what he thinks *should* be taught to what is practically possible. But in the best biological departments (certainly in the best botanical ones) it has been the practice for many years to have a set of independent "advanced" courses given by people who are more or less specialists in their subjects, and this plan, as Prof. Huxley says, has the great advantage of presenting different characteristic points of view, and enabling the student to find out which attracts him most. What seems to the reviewer a more difficult and pressing practical problem is to decide the nature and contents of the introductory course, which should be full enough to open avenues to the different "advanced" developments of the subject. It is common ground that a survey of the main facts of structure and development must be the foundation, but there are very different ways of elaborating the teaching of these, ways which may give the most various kinds of bias to the nature of the student's interest in the subject. We are, in the reviewer's opinion, nowhere near finality in this matter, but it is clear that the practice of giving the student an exclusively morphological bias can hardly any longer be defended. With all due respect to the advantages of the stable and "well tried," we need varied experiments in elementary teaching.

It is encouraging to note that Prof. Huxley, who would probably not call himself an ecologist, is of opinion that "Ecology is destined to a great future" in regard to applied economic work. He warns us of the danger of seeking too exclusively for specific knowledge of economic problems and specific remedies for economic ills. Branches of study like economic entomology and mycology, as has often recently been pointed out, are really all special

applications of ecology, and a broad ecological training is the only sound foundation for those who will be concerned practically in the field with the solution of the numerous economic problems which are concerned with living organisms on which the welfare of mankind is coming more and more to depend.

A. G. T.

Rayner, M. C. *Mycorrhiza, an account of non-pathogenic infection by Fungi in Vascular Plants and Bryophytes.* Pp. x + 246, with 64 figures. *New Phytologist* Reprint, No. 15. Wheldon and Wesley, Ltd., 2-4 Arthur Street, New Oxford Street, London, W.C. 2. Price 21s.

A general account of Mycorrhiza has long been needed, especially in view of the modern exact experimental work on the subject, work which has gone far to replace the rather insecure theories of thirty or forty years by soundly established conclusions, and has begun to throw light on the actual nutritional relations between fungus and host in this important type of association between two widely different organisms. Dr Rayner is well known for her researches on the endotrophic fungus of *Calluna vulgaris* and other Ericaceae, and she has now placed a wide circle of readers in her debt by contributing this very full historical account (which appeared in *The New Phytologist* during 1926 and part of 1927, and is now issued as a separate volume) of the relations of non-pathogenic fungi with the higher plants.

The opening chapter deals with what the author calls the "Early Period," from about 1840 to 1880, mainly of historical interest, though the author has unearthed some significant early work and reproduces figures from Lees and Rylands, published in *The Phytologist* in 1844, of the mycorrhiza of *Monotropa*. The "Second Period," from 1880 to 1900, to which the second and third chapters are devoted, includes the important work of Frank, who invented the name *mycorrhiza*, made very extensive observations on it in various plants, and put forward a theory which, though it lacked experimental support at the time, has been on the whole strikingly confirmed by the most recent work. These first three chapters are of special excellence—the subject is developed in a clear and masterly manner, and the relative importance of the contributions of the various workers exceedingly well brought out.

The "Modern Period," from about the beginning of the century to the present time, is marked by the opening up of several new lines of attack. Beginning with Stahl's well-known paper in the *Jahrbücher für wissenschaftlichen Botanik* (1900), which, as the author remarks, is the work most quoted in text-books, probably because it covered a wide field and put forward a clear and plausible general theory of the subject, the modern period is illuminated especially by Bernard's work on the mycorrhiza of orchids, by the author's own on Ericaceae, and finally by Melin's excellent recent researches on the mycorrhiza of forest trees. It is also marked by the strong advocacy, on the part of several writers, in opposition to Frank's thesis, of the view that mycorrhiza is really a phenomenon of parasitism, and cannot be regarded as of advantage to the vascular plant invaded by the fungus. It seems to the reviewer that the polemic on this subject is partly sustained by too teleological a view of such phenomena. It often seems to be implicitly assumed that we must either be dealing with a straightforward case of aggressor and victim, or else with a co-partnership which is almost invested with the nature of a conscious bargain for mutual advantage. In reality, of course, there must be every degree of transition between the extreme case where a parasite attacks (and kills) a "host," and a delicately adjusted equilibrium between two organisms which continue to live in intimate connection because the forces tending to maintain each in its relation to the other are accurately balanced. To try to analyse such a relationship primarily in terms of "advantage" to the two organisms is certainly not the way to understand its real nature. But in fact Melin's work does seem to make quite definite "advantages" overwhelmingly probable, both to fungus and tree, in the case of typical ectotrophic mycorrhiza,

though that conclusion does not in the least exclude the possibility of relations between fungi and roots where no such clear permanent "advantages" exist on either side.

If we may venture a word of criticism of the middle chapters, it is that the long accounts of Bernard's and especially of Melin's work are too diffuse, and would have been greatly improved by more pulling together and summarisation. In the account of Melin's work particularly there is a good deal of repetition, and the conclusions are not always quite clear. A table showing the species of the Hymenomycetous Fungi which (1) have been proved experimentally to be mycorrhizal symbionts of the different forest trees and (2) are most probably so, would have been very welcome.

There are useful chapters on fungal symbiosis with Bryophytes and Pteridophytes and an interesting one on the formation of "tubers" or "tubercles" as a result of fungal and bacterial attack. Finally there is a good summary of the evidence to date on the physiological nutritive relation between fungus and host, and a bibliography of more than 550 titles.

The work will not only be very useful as a summary of our knowledge to special students of mycorrhiza, but also to mycologists at large, to students of the physiology of nutrition, to ecologists and to scientific foresters.

A. G. T.

THE ECOLOGY OF MT. WILSON, N.S.W.

McLuckie, J. and Petrie, A. H. K. "An Ecological Study of the Flora of Mount Wilson. Part iv. Habitat Factors and Plant Response." *Proc. Linn. Soc. of New South Wales*. 55 pp. With 20 figures in the text. 1927.

The final part of this study recounts detailed investigations into the habitat factors which control the distribution of the vegetation types of Mount Wilson and the plant response to these factors. As has been previously indicated, the change from one type of vegetation to another is generally abrupt even within a small area: the climatic factor, it is pointed out, cannot be responsible for this, as neither the rainfall nor the general regional features of climate and season vary to any marked extent over the area in question. A general account of the temperature, rainfall, and humidity is given. For ascertaining the evaporating power of the air, Livingston atmometer cups were not available and evaporimeters were made from Chamberlain filter-candles attached to burettes by a piece of rubber tubing, care being taken to exclude air bubbles, and to keep the filters above the level of the water column in the burette. This apparatus gave a rapid and accurate record of the water evaporated. Records were taken every twelve hours to obtain data for day and night periods respectively. The results of this series of experiments gave interesting confirmation of observations on the effect of exposure on the distribution of the various communities and it was ascertained that the distribution of types generally is not characterised by corresponding fluctuations in atmospheric humidity. Information as to the principal limiting factor was sought therefore in another direction, namely, the moisture-content of the soil, and here it was found that the distribution of the *Ceratopetalum-Doryphora* association is determined by water-content of the soil, apparently independent of soil type. This, however, in its turn is subject to control by the exposure and the prevailing atmospheric humidity, so that this association is not always found where it might be expected from high percentage of soil moisture. The other types of vegetation appear to be limited in the first instance by this factor also. The case is summarised as follows. "The comparison of the soil-moisture values of this series of communities indicates clearly how the zonation of vegetation tends to coincide with a zonation of soil-moisture. There is no doubt that the falling gradient is increased by the progressive decrease in the capacity of the vegetation to conserve soil-moisture by shade and humus production. It appears then that the *Ceratopetalum-Doryphora*, *Eucalyptus goniocalyx*-*E. Blaxlandi* and *E. piperita*-*E. haemastoma* var. *micrantha* associations are adapted to habitats of decreasing soil-moisture content: each will occupy the

habitat where it finds its range, provided the other controlling factor of exposure permits; if this does not, one of the following associations in the series will occupy the habitat. The more xerophytic communities are no doubt excluded from the more mesophytic habitats by competition."

In investigating the physical structure of the soil the interesting fact was found that there was little difference between the effect of the sandstone and the clay soil of the basalt. This is explained by the clay fraction of the basalt soil being able to hold sufficient moisture to provide a suitable substratum for the development of a rich humus, aided by shade and humidity of the Rain Forest. The hydrogen ion concentration of the soil solution was proved to be not a factor of significance in the distribution of these types of vegetation.

In the results of investigations into plant-response it is stated that members of the same family, growing under precisely the same conditions in the same locality, show, amidst a general similarity of response, certain individual differences. Detailed studies of the leaf structure of the chief constituents are given with illustrations.

Studies of the root-systems, so far as they have been undertaken, show that they correspond to the conditions of aeration of the soil. No types of the Rain Forest appear specially adapted to deep penetration in the soil, whilst the roots of the sclerophyllous sandstone types have had to penetrate deeply.

In summarising the results of this study the authors emphasise the point that distribution of the communities is correlated with the edaphic water supply. The Rain Forest is to be regarded as a vestigial remnant of a former vegetation of widespread range in eastern Australia which has now retreated to such habitats as furnish it with optimum conditions. As the basalt caps of the sandstone are slowly carried away by geological denudation, the area of this Malayan forest will gradually shrink before the dominance of the autochthonous flora.

T. F. C.

A BOTANICAL GUIDE BOOK TO THE VICTORIAN GRAMPIANS.

Audas, James Wales. *One of Nature's Wonderlands: the Victorian Grampians.* 7 × 4½ in. Pp. 128 + xiv, with numerous photographic plates of plant and scenery. Ramsay Publishing Pty, 203 King Street, Melbourne. 1925.

The Victorian Grampians are situated between 100 and 150 miles WNW of Melbourne, almost on the main Melbourne-Adelaide railway line. They are a sandstone complex with some volcanic rocks, of no very great height, Mount William, the highest peak, being 3830 feet in altitude, though there are many peaks of over 2000 feet. The scenery is strikingly varied and beautiful and the flora very rich, the whole country being very sparsely inhabited and largely unspoiled and a great variety of native animals, including *Ornithorhynchus* and *Echidna*, still occurring in considerable numbers. The object of this little book is to make the country better known to visitors. The author is an accomplished botanist who has explored the district thoroughly and has discovered several species of plants new to science and many new to Victoria, within its confines. Mr Audas describes the region by giving an account of several of the excursions he has made in these mountains, writing pleasantly of the scenery, the inhabitants, the uses to which parts of the country have been put, and very fully of the interesting plants he collected. Features of the book are a series of excellent photographic plates of scenery and of individual plants, and a full index of scientific and common Australian names of the plants mentioned. It is a pity that the map is not larger and clearer.

A. G. T.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

BY CHARLES ELTON

THE literature bearing upon problems in animal ecology is extremely diffuse and scattered, with the result that a great deal of useful work is liable to pass unnoticed, or to become buried in journals which are not to be obtained at the ordinary libraries. This danger is particularly evident in the case of the numerous journals of natural history which flourish all over the British Isles, and which form an enormously important instrument for the recording of notes on the ecology of animals. Probably few people realise that there are more than sixty journals of this kind, most of them being the official organs of local natural history societies. The reader of these journals is constantly struck with the fact that professional scientists quite reasonably hesitate to publish any important work in them since to do so would be to bury their results almost completely. Very few people, outside the area covered by one of these journals, will take the trouble (even if they have the time) to go and get the journal out of one of the four big libraries in which they can be consulted, unless their attention is drawn to the existence of some particular paper in which they are interested; people in foreign countries cannot do so even if they would. It is proposed, therefore, to notice in the *JOURNAL OF ECOLOGY*, with the cordial approval of the Editor, any papers or notes of particular interest to animal ecologists, in order to try and bring these local journals to some extent into the general circulation, and make such ecological work available to professional scientists. A second reason for having some system of references or abstracts in the chief ecological journal is that it may give some kind of a lead to local naturalists, which may indicate to them the type of observation which is most urgently required in order to build up a system of scientific principles in animal ecology. It is an unfortunate fact that more than half the observations which are published in local journals of natural history are of definitely low grade, and often quite useless. This applies with especial force to lists of animals from counties, or from other arbitrary areas such as urban districts, in fact to almost any of the long lists, without any habitats or other ecological data, which are so frequently published. Of course, people have a certain amount of right to print anything which gives them pleasure, but one's impression is that these observations are usually published with the idea of being of some use to other people. The papers which have been selected in the present system of references are chosen in order to show the kind of work which is of most use in animal ecology (as far as can be seen at the present moment), and also to illustrate the best methods of

working and of recording the facts discovered. Ecological work on animals is still in a rather early stage of development, and every year one sees some entirely new idea or method brought into operation; but in spite of this, it is possible to indicate in a general way the most profitable methods to be adopted in working on the subject. The making of local lists and clearing up of the systematics of different animal groups form the first stage, which has been reached some time ago in most places. Next comes the stage of carrying out accurate ecological surveys, which comprise exact notes on the animal associations found in different habitats (e.g. in the various plant associations). The third stage is the study of the food-habits of all the different animals, in order to be able to draw up a general scheme illustrating the interrelations of the species. Each community of animals is then found to have its characteristic food-cycle, which varies from time to time, but is still characteristic in its variations. When this has been done (and it has been done in very few cases), the ecologist is in a position to tackle problems concerned with animal numbers; for the way in which animal communities are organised throws light on the means by which the numbers of the animals are controlled. Here the animal ecologist comes in contact with the economic zoologist, who is thirsting for some general principles to employ when he is faced with any of the innumerable problems which depend for their solution on the control of animal numbers. Another side to this fundamental ecological work is the working out of the autecology of single species, and the factors which affect their life-histories and which limit their distribution and numbers. The local natural history societies provide an organisation whose potentialities have not yet been fully realised, except by meteorologists, who have sometimes used them to record phenological observations. The same thing could be done as regards organised ecological work, except that the latter would be tremendously useful while the phenological work is largely of fictitious value. The list of references given below, together with a second instalment which will be published in the next number of this JOURNAL, will attempt to cover all important ecological notes on animals published in local journals since January 1926. Any system of abstracts is bound to be one-sided and incomplete, and this one will be no exception; the two chief objects which have been borne in mind are to leave out no note which affords data *that can be used by other people* (so much of interest is not recorded with sufficient fulness or accuracy to be of much real use), and secondly, to point out the sort of information which is needed. In addition to the others, a certain number of important papers from the larger scientific journals have been included, on account of their ecological interest, and as examples.

1. GENERAL PAPERS ON PARTICULAR GROUPS OF ANIMALS.

Edwards, F. W. "On the British Biting Midges (Diptera, Ceratopogonidae)." *Trans. Ent. Soc. (London)*, **74**, pp. 389-426. 1926.

A revision of the systematics of the group, with some notes on the habits (e.g. blood-sucking habits) and habitats of the larvae and adults.

Edwards, F. W. "A Synopsis of British Bibionidae and Scatopsidae (Diptera)." *Ann. Applied Biology*, **12**, pp. 263-275. 1925.

Gives keys down to species, with notes on the habits of the flies and their larvae. Mentions that *Dilophus febrilis* is one of the most important agents in the fertilisation of fruit blossom.

Pearman, J. V. "A Short Account of British Psocids." *Annual Report and Proc. Bristol Nat. Soc.*, **6**, pp. 222-228. 1927.

The first connected general account of these insects in Britain since 1867. Gives keys to the twenty-seven genera. These animals are an important "key-industry," feeding on algal and fungal growths on bark of trees and other places, and are at their greatest abundance in the summer months.

2. ECOLOGICAL SURVEYS, AND HABITAT NOTES.

Walton, C. L. "Insects Attacking Potatoes in North Wales." *Ann. Applied Biology*, **12**, pp. 529-535. 1925.

Survey of the important insects found on potatoes at a number of stations from sea-level to over a thousand feet, and in various environments. Springtails and aphids were the most abundant animals; it is important to note that one species of springtail (*Bourletiella lutea*) occurred very abundantly, feeding on the green leaves, whereas most springtails seem to be scavengers or eat fungae, pollen, etc. There are very interesting notes on the variations in the number of aphides from year to year, depending upon the dryness of the summer, e.g. hardly any in the hot dry 1921, increase during 1922-3, with a maximum in 1925.

Brown, J. M. "The Collembola of Derbyshire and Yorkshire." *The Naturalist*, pp. 333-335. Nov. 1926.

Complete lists, with a certain amount of ecological data about the species.

Womersley, H. "The Apterygota of the South-West of England." Part 3. *Annual Report and Proc. Bristol Nat. Soc.*, **6**, pp. 217-221. 1925.

Gives the exact habitats of a number of springtails.

Cuthbertson, A. "Crane-flies of the Inner Hebrides." *Scottish Naturalist*, pp. 53-58. 1926.

Gives lists for some of the islands, together with very good ecological data, based on collecting, and on breeding out larvae. There are also a number of other valuable notes, e.g. *Scatophaga* capturing the crane-fly *Gonomyia dentata*; web-spider *Meta menanae* catching *G. dentata*, *Dicranomyia*, etc.; the association of insects living in wet mud by stream margins; spiders (*Lycosa pullata* and *Pirata piratica*) catching *Trichocera*, *Gonomyia* and *Dicranomyia*.

Fox Wilson, G. and Hort, N. D. "Insect Visitors to Sap-exudations of Trees." *Trans. Ent. Soc. (London)*, **74**, pp. 243-251. 1926.

Study of the insects (flies, bees, wasps, butterflies, etc.) feeding on sap-exudations from an oak tree in Surrey, with a few notes on the birds that eat the insects. Also contains a good survey of the other work on this subject, and a discussion of the nature of the stimulus which attracts the insects.

- Quick, H.** "Oecological Notes on the Oxwich Sand-dune Area." *Journ. Conchology*, **18**, pp. 119-122. 1927.

Lists of molluscs, with good ecological data on the habitats and plant species.

- Ellis, A. E.** "Notes on Some Land Mollusca from Land's End." *Proc. Malacol. Soc.*, **27**, pp. 123-126. 1926.

Lists from various habitats, of which accurate notes are given, especially as regards plant species.

- Nicholson, C.** "Bugs, with Special Reference to the Epping Forest Area." *Essex Nat.*, **21**, pp. 169-185. 1926.

List of land and freshwater Hemiptera of this area, with many good notes on the habitats of the species.

- Gardiner, A.** "Ecology Notes on the *Zostera* Beds in the Helford River, Cornwall." *Journ. Conchology*, **18**, pp. 147-148. 1927.

Careful survey of the mollusca, with some notes on other animals, e.g. geophyean worms.

- Gardiner, A.** "The Parasites of *Modiolus modiolus* (Linné)." *Journ. Conchology*, **18**, pp. 143. 1927.

List of animals (hydroids, sponge, serpulid worms) living on this bivalve, and also in it (a crab and a polychaete worm), off the South Sands at Tenby.

- Lister, G.** "*Badhamia populina* (Lister) at Walthamstow." *Essex Nat.*, **21**, p. 133. 1925.

Notes on the Mycetozoa occurring on poplar logs.

- Soar, C. D.** "On the Recent Occurrence of an Halacarid, a Rare Water Mite, in Epping Forest." *Essex Nat.*, **21**, pp. 59-61. 1925.

Draws attention to the fact that there are some Halacarid water mites, which occur sometimes in freshwater, although this group is normally marine.

- Merritt Hawkes, O. A.** "A Preliminary Account of the Life-history of *Coccinella 11-punctata* (L.)." *Trans. Ent. Soc. (London)*, **75**, pp. 47-52. 1927.

Most lady-birds and their larvae feed on aphides; this species is shown to have a larva which lives on dung, and has a carnivorous adult stage. Good account of food-habits and some of its enemies, throughout its life.

- Burkill, H. J.** Entomological Section, *London Naturalist*, pp. 39-41. 1926.

Records the grasshopper, *Meconema thalassinum*, ovipositing on pine trunk in Surrey. It is usually found on oak trees.

- Chopra, R. L.** "On the Structure, Life-history, Economic Importance and Distribution of the Cocksfoot Moth, *Glyphipteryx fischeriella* Zell." *Ann. Applied Biology*, **12**, pp. 359-397. 1925.

Complete notes on life-history, food-habits, and times of activity of this moth, which eats the seed of the grass.

Gardiner, A. "Habitats of *Trivia arctica* (Montg.) and *Trivia monacha* (da Costa)." *Journ. Conchology*, **18**, p. 142. 1927.

The former species lives only in *Zostera*, the latter on low water rocks only.

Elmhurst, R. and Stephenson, J. "On *Lumbricillus scoticus* n. sp." *Journ. Marine Biol. Association*, **14**, pp. 469-473. 1926.

An Enchytraeid Oligochaete worm living between tide-marks on the shore of Cumbræes in Scotland, and feeding on the seaweed *Ascophyllum nodosum*.

Boycott, A. E. "Oecological Notes, No. 10. Transplantation Experiments on the Habitats of *Planorbis corneus* and *Bithynia tentaculata*." *Proc. Malacological Soc.*, **27**, pp. 156-158. 1927.

Proves that the snail *P. corneus* survives in many cases when moved from flood-plain ponds to isolated ponds from which it is usually absent, and therefore that its distribution is partly limited by dispersal difficulties. *B. tentaculata* did not survive for more than a few years, when similarly transplanted.

3. FOOD-HABITS.

Andrews, H. W. "British Asilid Flies and their Prey." *Proc. Ent. Soc. (London)*, **2**, pp. 13-14. 1927.

Several exact records.

MacDonald, R. "Food and Food-habits of *Meganyctiphanes norvegica*." *Journ. Marine Biol. Assoc.*, **14**, pp. 753-784. 1927.

This Euphausiid crustacean is an important link in the marine food-chain leading from detritus, algae, and protozoa, up to fish, e.g. the herring. An important account of its food and enemies in the Clyde Sea area; also contains useful notes on other animals (e.g. parasites) associated with it.

Hamm, A. H. and Richards, O. W. "The Biology of the British Crabronidae." *Trans. Ent. Soc. (London)*, **74**, pp. 297-331. 1926.

Summary of all known exact records of the food-habits and parasites of these predaceous digger-wasps. Includes also a survey of continental literature on the subject. Very important contribution to our knowledge of British animal communities.

Harvey, H. W. "Nitrate in the Sea." *Journ. Marine Biol. Assoc.*, **14**, pp. 71-88. 1926.

Shows that nitrates in the surface water of the English Channel are scarcer in summer than in winter, and probably limit the growth of phytoplankton, and therefore also of zooplankton. Discusses the nitrogen cycle in the sea.

Hibbert-Ware, A. "Marsh Tit Eating Woundwort Nutlets." *Essex Nat.*, **21**, p. 132. 1925; and "Titmice Eating Poppy Seeds." *Loc. cit.*

The latter refers to Blue and Great Tits.

Main, H. "Notes on *Methoca ichneumonides*." *Essex Nat.*, **22**, pp. 1-5. 1927.

Describes the habits and life-history (with the aid of very good photographs) of this hymenopteron, whose larva is parasitic on the larvae of tiger-beetles (*Cicindela*).

Moffat, C. B. "The Hedgehog." *Irish Naturalist's Journal*, **1**, pp. 45-47. 1926.

Notes that the hedgehog eats large numbers of the big black slug (*Arion ater*), which is rejected by nearly every kind of bird.

Glegg, W. E. "Epping Forest Report." *London Nat.*, pp. 35-36, 1926; and p. 56, 1927.

List of birds and other animals eaten by a pair of sparrowhawks, derived from the feathers and other traces left at their killing place. Besides birds, ground beetles (*"Abax striolatus"*) were often eaten.

4. THE NUMBERS OF ANIMALS.

Orton, J. H. "On Lunar Periodicity in Spawning of Normally Grown Falmouth Oysters (*O. edulis*) in 1925." *Journ. Marine Biol. Assoc.*, **14**, pp. 199-224. 1926.

The oysters show a marked tendency to breed about the time of the full moon; the probable causes of this are discussed.

Robbins, R. W. "Rabbits and Butterflies." *London Nat.*, pp. 37-38. 1927.

A colony of chalk-hill blues (*Agriades coridon* and *A. thetis*) in one locality on the east Surrey downs, was wiped out because rabbits ate out their food-plant, *Hippocrepis comosa*. This, in turn, was caused by local over-increase in the rabbits.

Ware, W. M. "A Disease of Wild White Clover caused by the Eelworm, *Tylenchus dipsaci* (Kuhn) Bastian." *Ann. Applied Biol.*, **12**, pp. 113-119. 1925.

Ritchie, J. "Note on Coccidiosis of Brown Hare (*Lepus europaeus*) in 1925." *Trans. and Proc. Perthshire Soc. of Nat. Science*, **8**, pp. 156-157. 1926.

Heavy autumn epidemic in many parts of Perthshire, caused by coccidian infection.

Baxter, E. V. and Rintoul, L. J. "Report on Scottish Ornithology in 1925." *Scottish Nat.*, pp. 69-84. 1926.

In this report the variability in numbers and instability in range of the birds are emphasised. For instance, the Green Woodpecker is spreading in Scotland; there was an "extraordinary increase in the number of Reed Buntings" in certain places in 1925; all tits were very scarce after the bad winter of 1917, but are now on the increase again, the Great Tit having reached its former high numbers.

Baxter, E. V. and Rintoul, L. J. "Some Effects of Hard Weather on Bird Life in East Fife." *Scottish Nat.*, pp. 5-6. 1926.

Hard frosts and heavy snow in November and December 1925 caused deaths among some birds, and changes in the food-habits of others.

Scourfield, D. J. "Water turned to 'Blood' in an Epping Forest Pond." *Essex Nat.*, **21**, pp. 154-157. 1926.

Tremendous multiplication of a small flagellate, *Chromatium okenii*, together with sulphur bacteria, in September 1924, and again in the same month in 1925.

BRITISH ECOLOGICAL SOCIETY

MEETING AT KEW GARDENS.

By invitation of the Director (Dr A. W. Hill, F.R.S.) the Society met at Kew on June 11th, 1927. The afternoon was spent in the Herbarium and Experimental Ground and the evening in the Gardens. The members were the guests of the Director to tea in the interval.

The Keeper of the Herbarium (Mr A. D. Cotton), having welcomed the Society to Kew, emphasised the importance of ecology to the studies which were the main feature of botanical work at Kew and expressed a hope that in the future there would be a closer connection between Kew and the Society.

EXHIBITS OF SCLEROPHYLLOUS VEGETATION.

Mr Cotton indicated that the principal exhibit was a composite one prepared by members of the Herbarium staff and designed to illustrate, by means of living and dried specimens, pictures and maps, certain of the sclerophyllous brushwood communities of countries having a Mediterranean type of climate. The exhibits were then demonstrated in turn and a summary of the remarks is given below.

1. *Mediterranean.*

Mr W. B. TURRILL stated that the essential features of the Mediterranean climatic type are the winter rains and summer drought. It is important to emphasise that it is not the total annual rainfall which is significant but its seasonal distribution. This can best be illustrated by two graphs drawn to the same abscissae for the months and to ordinates for inches or centimetres of rainfall and degrees of temperature respectively. It is the occurrence of marked wet and dry seasons and the coincidence of the hottest and driest periods that define the "Mediterranean" climate. Correlated with this climatic type we find that all those areas which it characterises have sclerophyllous brushwoods well developed. These differ, especially floristically, in the different areas, yet in physiognomy they show strong and ecologically important similarities. No attempt had been made in preparing the exhibits to correlate structure and habitat in any detail but rather to give a bird's-eye view of the floristic composition and habit of hard-leaved shrub communities in five areas chosen from five continents.

The chief sclerophyllous vegetation of the Mediterranean Basin is the well-known maquis or macchia, which occurs on most of the Mediterranean seaboard of South Europe and in parts of Asia Minor and North Africa. A map illustrates the fact that the Mediterranean Basin is divided into two subsidiary basins, and there are differences in the climate of these two basins, the eastern, lying farther south, being, on the whole, the hotter and drier. Correlated with this there are differences in the macchie of the two basins, although these differences mostly concern subordinate elements. The exhibit illustrates the eastern macchie as represented in the Balkan Peninsula. Macchie occur in all the true Mediterranean districts of the Balkan Peninsula. In Crete and Greece they reach inland and to over 1000 m. altitude. In other districts they are limited to the coastal parts, often overhanging the sea-water. Their distribution north of Greece is not without interest. Along the Adriatic they stretch with a considerable degree of continuity through Epirus, Albania, Montenegro, Hercegovina, and Dalmatia. There is a break in Southern Croatia and the Quarnero Gulf, but they reappear in a somewhat depauperated form in Southern Istria where the speaker, in 1922, traced their final dying out about halfway up the west coast. In Istria they occur only on limestones, but where arenaceous rocks outcrop they are absent. Relative to the

previous remarks on the climate, it was added that in Southern Hercegovina is the hottest place in Europe and on the Dalmatian-Montenegrin border is the wettest. All down the eastern Adriatic the total annual rainfall is abundant, but it nearly all falls in the winter months. On the Aegean coasts macchie occur in Thessaly, but only in the Khalkidike Peninsula in South Macedonia. They are found on the Thracian coast and very typically in the Gallipoli Peninsula, but east of this to the Bosphorus they only occur in a very depauperated form and are not known on the Black Sea coast.

Essentially the Balkan Peninsular macchie consist of hard-leaved evergreen shrubs or small trees. The luxuriance varies much, but the list of species is, for the Balkan Peninsula, a very definite one, and, though all do not occur in any one locality, the general composition has rather narrow limits of variation. The richness of the ground flora varies with the density of the shrub layer but is typically Mediterranean, and mostly early spring flowering with many geophytes.

The most characteristic macchia shrubs of the area are: *Arbutus unedo*, *A. andrachne*, *Myrtus communis*, *Olea europaea*, *Juniperus phoenicea*, *J. oxycedrus*, *Phillyrea latifolia*, *P. media*, *P. angustifolia*, *Quercus ilex*, *Q. coccifera*, *Pistacia lentiscus*, *P. terebinthus*, *Cistus villosus*, *C. salviifolius*, *Calycotome infesta*, *C. villosa*, *Laurus nobilis*, *Smilax aspera*, *Ruscus aculeatus*, *Erica arborea*, *E. verticillata*, *Rosmarinus officinalis*, *Ceratonia siliqua*, *Asparagus acutifolius*, and *Viburnum tinus*.

It will be noticed that broad-leaved sclerophyllous plants are well represented.

Mr Turrill distinguished four types of macchie, as follows:

1. Undergrowth to *Pinus halepensis* forest, here forming a layer society.
2. Brushwood from which *Pinus halepensis* has been cut out and shows no sign of rejuvenating and the macchia itself tending to degenerate to phrygana or rock-heaths.
3. Brushwood becoming more luxuriant and leading to either 1 or 4 as a climax, primary or secondary, i.e. macchia as an associates.
4. Brushwood, without trees, stable and a climatic climax association.

These types were distinguished by their developmental history and relationships. Floristically each type shows the same range of variation, except that 2 is usually poorer. Thus a community of the same taxonomic composition may be a layer society, an associates, or an association.

On the Adriatic and Greek coasts the first and second types are particularly common, while the third and fourth are, now at least, decidedly rare, and probably only occur where protection from flocks and herds and from cutting is enforced. In Dalmatia and Southern Hercegovina the second degenerating type is the commonest and, indeed, it is difficult to draw any line between depauperated macchie and stony or rock "heaths." In the central part of the Lapad Peninsula a macchia of the third type and exceedingly luxurious was illustrated. In Western Istria, near the northern limit of macchie, some which represent a climax community north of the natural range of *Pinus halepensis* were quoted from personal knowledge.

Naturally macchie merge into pseudomacchie, so well represented in South Macedonia, or, more rarely, are replaced rather abruptly by shibljak.

Finally, it was mentioned that all of the living plants of the macchia shown had been grown out-of-doors at Kew. On the whole, they had lost some of their hard-leaved character under the condition of the English climate, but they showed a surprising degree of hardness under cultivation there.

2. Californian.

Miss M. L. GREEN then compared the broad sclerophyll vegetation of California with the macchie of the Mediterranean, and her exhibit was set out to illustrate this as far as possible. In California the term macchia is replaced by chaparral, the two communities

being ecologically equivalent. Miss Green dwelt on the chief features of the broad sclerophyll forest community and the chaparral, and showed how the plants growing there were adapted to their environment. The broad sclerophyll forest occurs in situations having an annual rainfall of from 10 to 30 inches, and is dominated by trees, whereas the chaparral occurs in drier situations up the slopes of the mountains, and is made up chiefly of shrubs. The chief trees of the broad sclerophyll forest which were exhibited either by fresh material or dried specimens were: *Castanopsis chrysophylla*, *Myrica californica*, *Quercus chrysolepis*, *Q. agrifolia*, *Q. engelmannii*, *Q. densiflora*, *Q. wislizenii*, *Q. kelloggii*, *Q. lobata*, *Umbellularia californica*, and *Arbutus menziesii*. It was pointed out how very similar these plants were to many in the Mediterranean exhibit of the broad sclerophyll macchia, attention being drawn particularly to *Quercus* and *Arbutus*.

The chaparral formation was represented by the following species, some of which occur in the broad sclerophyll forest formation: *Quercus chrysolepis*, *Q. dumosa*, *Q. wislizenii* var. *frutescens*, *Cercocarpus betulaeifolius*, *Adenostoma fasciculatum*, *Prunus ilicifolia*, *Rhus integrifolia*, *R. laurina*, *R. ovata*, *Rhamnus californica*, *Ceanothus crassifolius*, *C. cuneatus*, *Arctostaphylos andersonii*, *A. glauca*, *A. hookeri*, *A. manzanita*, *A. montana*, *A. pumila*, *A. stanfordiana*, *A. tomentosa*, and *A. vestita*.

3. Chilean.

Mr T. A. SPRAGUE demonstrated the sclerophyllous woody vegetation of Chile, remarking that broad-leaved sclerophyllous vegetation is much more poorly represented in Chile than in the Mediterranean or California. In Schimper's *Plant Geography* only half a page of text is devoted to it. In Northern Chile the rainfall ranges from a third of an inch to an inch and a half, and the vegetation is extremely xerophytic in character. In Southern Chile rains occur at all seasons. The sclerophyllous scrub and woodland are consequently confined to Central Chile, where the rains are in the winter season, and are chiefly developed between 30½° and 35° S. Even there they are limited mainly to altitudes between 3300 and 6600 feet.

A typical sclerophyllous scrub occurs in the mountains near Santiago, about 33° S. At Santiago itself the average summer temperature is 65° and the maximum 87°, the average winter temperature 45° and the minimum 23°. But the daily variation may be enormous. On one winter's day (in August) the maximum temperature was 77° and the minimum 23°, or 9° below freezing point, a difference of 54°.

Humidity of the soil and atmosphere is apparently the most important factor. At Santiago itself the annual rainfall is about 13 inches. The summer rains are so poor that they hardly affect the vegetation. In the town itself snow falls about once in every five years. But in the mountain region above 5000 feet snow falls every year, and there is consequently a much larger supply of water.

The scrub in the mountains of Santiago is largely composed of a cactus, *Cereus quisco*, and a bromeliad, *Puya coarctata*. These will grow in the driest situations. Amongst them is a large number of more or less broad-leaved sclerophyllous shrubs. Three constant elements are *Quillaja saponaria*, *Kageneckia oblonga* (both Rosaceae) and *Lithraea caustica* (Anacardiaceae). Among other elements are another *Kageneckia*, three species of *Colliguaja* (Euphorbiaceae), *Schinus dependens*, *Aristotelia magui*, *Gardoa gilliesii* (Labiatae), *Baccharis rosmarinifolia*, and *Proustia pungens* (both Compositae).

In comparatively well-watered valleys sclerophyllous woodland occurs in which the chief elements are *Drimys winteri*, *Cryptocarya peumus*, and *Bellota miersii* (Lauraceae) *Eugenia chequen* and other Myrtaceae, and *Villarezia mucronata* in addition to *Lithraea caustica* and *Quillaja saponaria*.

In drier localities the more or less broad-leaved sclerophyllous shrubs have a greater or less admixture of microphyllous and spiny types, such as *Fabiana imbricata*, *Porlieria hygro-*

metrica, *Acacia cavenia*, *Adesmia arborea*, *Trevoa trinervia*, *Colletia spinosa* (both Rhamnaceae), and *Tetraglochin strictum* (Rosaceae).

It is extremely difficult to give any general description of the sclerophyllous scrub or woodland, because every separate area, travelling from north to south or from the coast to the interior, seems to have different edaphic or climatic conditions and a different composition of the vegetation.

The systematic composition of the sclerophyllous vegetation is interesting. As in California, important elements are represented by various Lauraceae, Rhamnaceae, Anacardiaceae, and Rosaceae. *Fabiana imbricata* strongly recalls *Erica arborea* of the Mediterranean.

There is sometimes great similarity in vegetative characters between very distantly related shrubs. *Valenzuela trinervis* (Sapindaceae) and *Schinus dependens* (Anacardiaceae) are very similar in general appearance. So are *Kageneckia angustifolia* (Rosaceae) and *Colliguaja salicifolia* (Euphorbiaceae).

4. Australian.

Mr V. S. SUMMERHAYES stated that sclerophyllous brushwood communities occur in South-western Australia and in the southern part of South Australia around Spencer Gulf, in both of which areas the winter rainfall predominates. Little detailed work had up to the present been done on these communities but there was no doubt that they agreed in general characters with the Mediterranean mallee. In South-western Australia sclerophyllous forests of *Eucalyptus marginata* (Jarrah) and *E. diversicolor* (Karri) occur near the coast where the rainfall is highest, while the Wandoo (*E. redunca*) is abundant locally. These forests have a sclerophyllous scrub layer, and farther inland, where the rainfall decreases, the trees disappear and the scrub takes the place of the forest. This, in its turn, passes into semi-desert and desert. It is difficult to describe in any detail the constitution of this scrub, since the extremely rich flora of South-western Australia contains a large number of local endemics. Different species of the same genus therefore replace one another in different parts of the area under consideration, but the general type and habit remains the same throughout. Plants with small ericoid foliage are relatively more abundant than in the Mediterranean, while deeply cut and spinous leaves are a marked feature. The chief families concerned are Proteaceae (species of *Banksia*, *Dryandra*, *Hakea*, and *Grevillea*), Myrtaceae (*Melaleuca*, *Darwinia*, etc.), Leguminosae (*Acacia*, *Gastrobium*, *Oxylobium*, *Pultenaea*, *Hovea*, etc.), but the species are exceedingly numerous. As in other similar communities, geophytes are prominent, consisting of various orchids and plants belonging chiefly to Iridaceae, Amaryllidaceae and Haemodoraceae. The striking Grass Trees or "Blackboys" (*Xanthorrhoea* spp.—Juncaceae), with stiff sword-like leaves, are characteristic of these communities.

5. South African.

Miss I. C. VERDOORN pointed out that the south-west portion of South Africa enjoys a Mediterranean climate and there one finds sclerophyllous communities as in other corresponding regions. Forests, consisting of trees with evergreen, mostly elliptical, leaves, occur in the ravines and on the more protected slopes of Table Mountain. In the Cape District, as this area is usually called, the characteristic feature of the sclerophyllous vegetation is the predominance of ericoid and pinoid types of leaf, these being more abundant relatively than in any of the other districts dealt with. Broad-leaved species, however, occur, such as *Leucadendron argenteum*, which forms open woodland on the slopes on Table Mountain, and many species of *Protea*, *Leucospermum*, etc., all of which have leathery leaves similar to the Mediterranean and Californian types. Among the ericoid types *Erica*, of which there are several hundred species, many Rutaceae, such as *Agathosma* and *Barosma*, a large variety of Leguminosae of which *Aspalathus* is the most prominent genus, *Phylica* (Rhamnaceae),

many Thymeleaceae and numerous Compositae, including *Helichrysum*, are the most important, while inland large stretches are covered by *Elytropappus rhinocerotis* (Compositae). Bulbous plants are also prominent, species of *Watsonia*, *Bobartia* and *Gladiolus* occurring frequently, together with many orchids.

OTHER EXHIBITS.

In addition to the above joint exhibit, a number of independent ones were also shown. Dr J. M. Dalziel demonstrated a series of specimens of genera and species of temperate climates occurring on the upper regions of Cameroons Mt. This mountain on the west coast of Tropical Africa, 13,300 feet high, is separated from the high mountains of Abyssinia and East Africa, 16,000–19,000 feet, by 1500–2000 miles of equatorial forest or of tropical savannah, and from Europe by the whole of North Africa which is mainly arid and hot. These mountains are therefore, in a phytogeographical sense, like islands. The flora of their upper slopes contains many temperate forms, belonging to families and genera common in Europe.

The forest on Cameroons Mt. ends suddenly at 6000–7000 feet elevation—one passes immediately on to grassy slopes. Before leaving the forest one finds species of the following temperate genera: *Thalictrum*, *Clematis*, *Viola*, *Impatiens*, *Trifolium*, *Rubus*, *Anthriscus*, *Unicula*, *Galium*, *Cynoglossum*, *Myosotis*, and *Sibthorpia*. Amongst these *Sanicula europea* and *Galium aparine* are common enough, and *Sibthorpia europea* is also found. The latter occurs also in North Africa.

On the higher grasslands, 7000 feet to summit, examples of the following families were exhibited as conspicuous: Cruciferae, Caryophyllaceae, Hypericaceae, Linaceae, Geraniaceae, Leguminosae, Rosaceae, Crassulaceae, Umbelliferae, Rubiaceae, Dipsacaceae, Boraginaceae, Scrophulariaceae, Polygonaceae, Myricaceae, Juncaceae, and Gramineae. The following species of these have been regarded as identical with British species: *Cardamine hirsuta*, *Cerastium viscosum*, *Radiola linoides*, *Scabiosa succisa*, *Vulpia bromoides*, *Bromus giganteus*, *Aira caryophyllen*, and *Luzula campestris*. *Scabiosa succisa* is common and virile on Cameroons Mt., but seems to be absent from Abyssinia and the other mountains of East Africa, and is not known with certainty from North Africa.

The total number of true British species found in all the mountains of this corner of West Africa may perhaps amount to about twenty.

Mr C. V. B. Marquand exhibited representative bryophyte components of a number of Arctic-Alpine Associations in Britain, particularly from Ben Hope in Sutherlandshire, and Teallach in Ross-shire, the Cuillians in the Isle of Skye, the Aonachs in Lochaber, as well as other better known mountains in England, Scotland, and Wales, on which he has carried out intensive studies for a number of years with a view to comparing the vegetation of our mountain tops with those of central and western Europe. The great wealth of the Arctic-Alpine bryophytes, as compared with the Phanerogams in this country, was emphasised, and mention was made of the importance of certain species of Mosses and Hepatics as index plants to climatic and edaphic conditions. Maps and photographs were shown of the vegetation of several areas in this zone which, it is believed, had not previously been explored bryologically.

Mr A. D. Cotton showed specimens of *Lycoperdon giganteum* which had been found under the floor of a drawing-room in a private house in the village of Kew. They were growing on the ground and the workmen who discovered them mistook them at first for a series of human skulls.

About half an hour was spent in the Experimental Ground attached to the Herbarium, where Mr W. B. Turrill referred to the establishment of the Ground in 1925 for the cultivation of plants of botanical interest from known localities and for studying by means of simple experiments some of the problems which arise in herbarium studies. The majority of the

species at present cultivated are representatives of the Balkan Peninsular flora and illustrate a considerable number of the dominant genera of this area. Amongst the more interesting plants pointed out were *Silene roemeri*, *S. densiflora*, *S. wolgensis*, *S. frivaldskyana*, *Onobrychis cana*, *Cerinth minor* var. *hispida*, *Veronica thracica*, *V. jacquinii*, *V. euzina*, *V. orchidea*, *Jurinea arachnoidea*, *J. transsilvanica*, *Ranunculus eriophyllus*, *Centaurea diffusa*, *Dianthus giganteus*, *Verbascum luteo-viride*, *V. bosniense*, *Salvia villicaulis*, *S. pratensis* var., *Campanula grossekii*, *C. lingulata*, *C. orphanidea*, *Armeria rumelica*, *Nepeta ucranica*, *Potentilla visianii*, *Heracleum ternatum*, *Lepidotrichum uechtritizianum* (two ecotypes), *Anthemis fussii*, *Satureia caerulea*, *Iris varbossana*, *I. mellita*, *Alyssum moellendorffianum*, *Peucedanum aegopodioides*, and various collections of *Silene vulgaris* showing a wide range of morphological features.

INSPECTION OF THE GARDENS.

In the evening, members made a tour of the Gardens under the guidance of Major Chipp (Assistant Director), when objects of special ecological interest were pointed out. In House No. 1 epiphytic orchids and Bromeliaceae were seen in natural settings, epiphytes with aerial roots, scandent Palmae, and Monocotyledons typical of the ground flora of the tropical forests. In Museum III examples of stilt-rooted Pandanaceae, strangling Figs and buttressed trees were the chief objects of interest. An excellent example of a woody liane (*Vitis*) was seen trailing around the verandah in the Palm House, where also a representative collection of Palmae was inspected. Tropical aquatics, including *Cyperus papyrus*, which forms the sudd of the Nile, were shown in House No. 15, and in the Temperate House the party had an opportunity of studying typical examples of the Australasian vegetation.

After tea the President proposed a vote of thanks to the Director and Staff of Kew Gardens, which was heartily accorded. The President expressed the gratitude which the Society felt for the kind hospitality that had been extended, and for the trouble that had been taken in the preparation of the programme and exhibits. Prof. Oliver and Prof. Fritch both spoke in support and voiced the general feeling of appreciation.

E. J. S.

SUMMER MEETING AT PICKERING.

A very successful meeting was held at Pickering from September 7th to September 12th inclusive. The Society is greatly indebted to the President, Dr Woodhead, and to the leaders of the various excursions for the admirable organisation of the meeting.

At the "White Swan," which constituted the headquarters, a large room had been placed at the disposal of the party, and here, on the first evening, Mr Root gave a succinct account of the geology of the areas to be visited. He particularly emphasised the important part played by glaciation in determining the local topography; the overflow channels of the glacial lakes being responsible for the flat-bottomed U-shaped valleys so characteristic of this region. The Jurassic rocks of the area show a great variety of lithological constitution, including non-calcareous grits and highly calcareous limestones, but the soils derived from these latter are often very completely leached. As a consequence, striking juxtapositions of "caldicole" and "calcifuge" vegetation are encountered.

On Thursday, under the guidance of Mr Burnley, the party visited the Hole of Horcum where the Dwarf Cornel (*Cornus suecica*) was seen growing freely amongst the ericaceous vegetation. The presence here of *Cornus suecica* at its southern limit in the east of England (on the west it occurs in S. Lancashire) is paralleled by the presence of *Trientalis europaea* and *Arctostaphylos uva-ursi*, which are also here almost at their southern limit (*A. uva-ursi* extends into Derbyshire).

In the evening Mr Highfield showed some excellent photographic studies of local species, and Dr W. G. Smith gave an account of the vegetation of the Cleveland area. On the following day Dr Smith, together with Mr Slater, acted as leader to the woods of Beck Dale. *En route* members visited the beautiful ruins of Rievaulx Abbey. The woods of Beck Dale, which were traversed from Rievaulx to Helmsley, are calcareous Ash-Oak woods, and among the more striking members of the flora may be mentioned *Actaea spicata*, *Helleborus viridis*, and *Hordeum sylvaticum*, all of which were present in considerable quantity. The marked variation in the soil conditions was, however, evident from the local occurrence of *Quercus sessiliflora* (in company with *Q. robur* and hybrids) associated with a ground flora in which *Pteridium aquilinum* and *Luzula sylvatica* were conspicuous features.

The following day was spent in examining the Allerston afforestation area under the guidance of Mr Ross, who, on the previous evening, had given an account of the work already carried out. The area acquired is about eleven thousand acres, of which a considerable portion has already been planted with Scots Pine, Spruce, etc. A striking example was seen of difference in growth on the opposite sides of a valley, probably due to the differences in water supply and nutrition consequent upon the dip of the strata being at a considerable angle to the direction of the valley. In this area Mr Ross had prepared for our inspection a number of pits which showed typical "pan" at a depth of about a foot.

On the Saturday evening Mr Burnley gave a lantern lecture on the Forge Valley area, which was visited on the Sunday under his guidance. Here members had the opportunity of seeing *Maianthemum bifolium* in its natural haunts.

The last day of the excursion, and one of the most interesting, was spent in visiting Newtondale under the guidance of Mr Flintoff, who provided refreshments for the party on reaching Levisham.

Owing to the departure of several members of the party on the Monday, an opportunity was taken on the Sunday evening to express the appreciation of those present to Dr Woodhead and the various leaders, who had spared no pains to contribute to the success of the excursion. Also our thanks were tendered to Dr and Mrs Kirk for their hospitality, and to the landowners for granting permission to visit their estates.

E. J. S.

ANNUAL MEETING, BIRMINGHAM, JAN. 6-7, 1928.

Members of the Society and a number of visitors were entertained at a *Soirée* in the Botanical Department on Friday, January 6th, at which various exhibits were shown and an opportunity was afforded of seeing the new science buildings and laboratories at Edgbaston. To the great regret of those present, the host of the Society, Prof. Yapp, was prevented by illness from himself receiving his guests. Mr Leach, however, acted as Prof. Yapp's deputy, and by his admirable arrangements secured the comfort and convenience of members.

The 14th Annual Meeting was held in the lecture theatre on Saturday, January 7th.

Dr Woodhead occupied the Chair and there was a good attendance both of members and guests.

The Minutes of the last Annual Meeting were read and confirmed, and the Hon. Treasurer presented the Accounts for 1927 (see p. 185), which were adopted. Mr Watt drew attention to the fact that the financial position of the Society showed a steady improvement, though the very satisfactory balance was largely due to sales of back-numbers of the *JOURNAL*.

A vote of thanks was accorded to Mr Paulson for acting as Hon. Auditor, and the meeting also expressed its appreciation of the continued efforts of Prof. Tansley, to which was due in no small measure the present satisfactory financial position of the Society. The Hon. Secretary presented his report, which was adopted.

HON. SECRETARY'S REPORT FOR 1927.

Four meetings have been held during the past year. The Annual Meeting took place on January 8th, 1927, in the Botanical Department of University College, London, when the President (Dr Woodhead) delivered an Address on the "History of the Vegetation of the Southern Pennines" and various other communications were made (see full report, *JOURNAL*, **15**, p. 181). On the previous evening members were entertained at a Soirée in the Botanical Department and the thanks of the Society are due to the many who helped towards the success of the evening either in personal assistance or by furnishing exhibits (see *JOURNAL*, **15**, p. 180).

On June 11th a most successful meeting was held at Kew, and it is much to be regretted that there was not a larger attendance to benefit by the exhibits and demonstrations that had been prepared with such care by the Director and Staff. After the meeting members were entertained to tea by Dr A. W. Hill. (For full report see this issue of the *JOURNAL*, p. 178.)

The Summer Meeting was held at Pickering immediately following the British Association and lasted from Wednesday, September 7th, to Monday, September 12th. Some 25 members were present and despite the very unsettled weather the meeting was an unqualified success, which we owe to Dr Woodhead's admirable organisation and the ungrudging assistance of the various leaders whose expositions in the field were helped materially by the evening addresses which preceded them. (For full report see this issue of the *JOURNAL*, p. 183.)

The question of undertaking transplantation experiments, referred by the General Meeting to the Council, was considered by that body, and a preliminary series of experiments with a few selected species is to be started at Potterne, Wilts., in Mr Marsden Jones' garden under the direction of a special sub-committee consisting of the President, Dr A. W. Hill, Mr E. Marsden Jones, Prof. Oliver, Dr Salisbury, Prof. Tansley (Chairman) and Mr Turrill. (See *JOURNAL*, **15**, p. 377.)

On Saturday, October 22nd, a fungus foray was held in conjunction with the British Mycological Society under the leadership of Mr Ramsbottom. Unfortunately there was on this occasion more opportunity for the study of high humidities than of the fungus flora.

Two numbers of the *JOURNAL* have been issued during the year, in February and August, together comprising 384 pages and ten plates.

During the year I have received notification of two resignations: seventeen new members have been elected, bringing our total membership to two hundred and thirteen.

E. J. S.

Mr Turrill reported on the activities of the Transplant Committee and stated that it was hoped to begin the experiments at Potterne, on four different types of soil with several species, in the early spring. On the proposal of Prof. Weiss, seconded by Mr Watt, a sum of £15 was voted by the Society towards the expenses of the scheme.

Dr Salisbury then presented the report of the Council with regard to the publication of a British Biological Flora in which biological and ecological data respecting British species would be brought together. A scheme prepared by Dr Salisbury was approved and the meeting unanimously resolved that such a Flora should be published by the Society under the editorship of Dr Salisbury. (See p. 161 of this issue of the *JOURNAL*.)

The following Officers of the Society were then elected:

PRESIDENT: Dr E. J. Salisbury.

VICE-PRESIDENT: Mr H. B. Watt.

HON. EDITOR: Prof. Tansley

HON. TREASURER: Mr H. B. Watt.

HON. SECRETARY: Dr E. J. Salisbury.

OTHER MEMBERS OF COUNCIL: Dr V. E. L. Anderson,
Prof. A. E. Boycott, Dr W. H. Pearsall.

Dr Woodhead then vacated the Chair in favour of the new President.

PAPERS.

The first paper was a communication by Mr C. S. Elton who gave an account of the animal communities of Spitsbergen. He emphasised the close parallel between the plant and animal communities and the importance of their interrelations. On the eastern side of the island both plant and animal communities were simple in character and composed of few species. With the low temperature and fog was associated a flora of lichens and mosses, supporting a sparse community of about nine animal species. With the ameliorating climatic conditions, as the west side of the island is approached, the complexity increases, till in the *Cassiope* heaths the number of animal species may be over fifty, whilst the individuals show a marked increase in numbers. Attention was drawn to the effect of birds in changing the character of the vegetation. In the discussion which followed Mr Summerhayes commented on the occasional absence of any apparent direct relationship between the fauna and flora, and Mr Paulson remarked on the reputed power of the reindeer to distinguish between *Cladonia rangiferina* and *C. sylvatica*, which the lichenologist had difficulty in separating.

Mr Leach then gave a short account of the vegetation of siliceous screes. He considered that the degree of mobility was the chief factor in determining the nature of the flora and emphasised the superficial character of the interstitial accumulations of soil. The pioneer species were usually cryptogams, especially lichens, which were followed by mosses and subsequently by rhizomatous species such as *Vaccinium myrtillus*. In the discussion, in which a number of those present took part, Prof. Weiss expressed the view that air-borne mineral matter was probably of considerable importance in determining the character of the interstitial material. Dr Pearsall thought that the succession was of a different character on screes of Skiddaw and Borrowdale slates. Dr Watson was of the opinion that lichens were usually the pioneers on the harder types of rocks, whilst mosses often played the same rôle on the softer rock types. *Gymnostomum donianum* was cited as very characteristic.

After lunch the following members were elected:

Miss M. K. Bishop; Mr R. Alun-Roberts; Miss G. F. Selwood; Dr C. J. Shirk; Mr P. Topham; and Mr R. E. Vaughan.

Miss M. K. Bishop then gave a preliminary account of some observations on the ecological relationships between various species of *Juncus*. These indicated that soil-aeration, soil-reaction and the mineral character of the soil were the most important factors involved.

The next communication was an account of observations on root-hairs by Dr Violet Anderson. Stress was laid on the remarkable diversity of their number and spatial distribution, their seasonal production in such plants as *Ulmaria filipendula*, and their diversity of structure. Liquified and pitted root-hairs are present in *Taxus fuccata*, whilst in *Anagallis arvensis* two strikingly different types of root-hair are present, a dimorphism which is more or less marked in other species. In the discussion which followed Dr Salisbury referred to the diversity of distribution in *Arachis hypogea* according to the conditions of growth, the functioning of the root-hairs of some Compositae for several years and the remarkable branched root-hairs that occur on the adventitious roots of *Helianthus rigidus*. The ecological importance of a study of root-hairs, which had been too much neglected in the past, was emphasised.

Dr Pearsall showed a series of photographs of the classical Lake Michigan sand dunes, the vegetation of which was originally described by Prof. Cowles (*Bot. Gaz.* 1899).

Prof. Oliver gave a summary of the early stages in dune formation of Blakeney Point. The embryo dunes are there formed around plants of either *Psamma* (*Ammophila*) *arenaria* or *Triticum* (*Agrophylum*) *juncum*. The former is comparatively intolerant of submergence by sea water, whilst the latter is a true halophyte. In *Psamma* the erect foliage affords less shelter to the surrounding sand than the drooping foliage of the *Triticum*, but the essential difference between them as early colonisers depends on the lateral branches of *Psamma* being ascending whilst those of *Triticum* are at first descending. In consequence of this the shoots of *Psamma* become exposed and wind-trimmed if the sand around is removed by a change in the direction of the wind whilst the shoots of *Triticum* remain unharmed.

After an adjournment for tea the meeting resumed, when Prof. Adamson showed a series of photographs illustrating the vegetation of Eastern Rhodesia. He called attention to the importance of the amount of rainfall, and to the effect of high water content and frosts in the valleys in restricting the savanna to the hill sides, the valley floors being occupied by tall grassland.

At the close of the meeting a hearty vote of thanks was accorded to Prof. Yapp for his hospitality and to Mr Leach for his admirable arrangements.

LIST OF MEMBERS (JANUARY, 1928).

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, DR E. J. SALISBURY, University College, Gower St, London, W.C. 1.

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FURTHER CONTRIBUTIONS TO THE ECOLOGY OF SPITSBERGEN

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(With Plates XXIV to XXXV, one Folding Map, and two Maps in the Text.)

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I. INTRODUCTION.

IN 1923 we gave an account of some of the plant and animal communities of Spitsbergen, seen and studied by us during the Oxford Expedition in 1921 (29). In the summers of 1923 and 1924, one of us (C. S. E.) paid further visits to the archipelago, on the Oxford Expeditions of those years, under the leadership of Mr George Binney, and had an opportunity of collecting further information about the plants and animals. Since quite different districts were visited and somewhat different problems encountered, it seems useful, first, to supplement and amplify the account already given, secondly, to attempt to draw certain general conclusions about the factors limiting the distribution of the communities, and thirdly, to attempt to relate the latter to those of other arctic

countries. Whereas in 1921 our ecological work was confined to the west coast and fjords of West Spitsbergen (see folding map), the expedition of 1923 concentrated chiefly on the regions of ice-pack around North-East Land and in Hinlopen Strait, visits being paid also to Wijde Bay and Liefde Bay. In 1924 a prolonged stay was made in Liefde Bay (Reindeer Peninsula), while members of the expedition's sledging parties brought back additional information from North-East Land. Short visits were also made in these two years to other localities, on the west coast and in Icefjord. For the details of the routes followed by the 1923 and 1924 expeditions we may refer the reader to Frazer and Relf (10) and Binney (2) respectively. A short account of the biological work done in 1924 was published by one of us in 1925 (7).

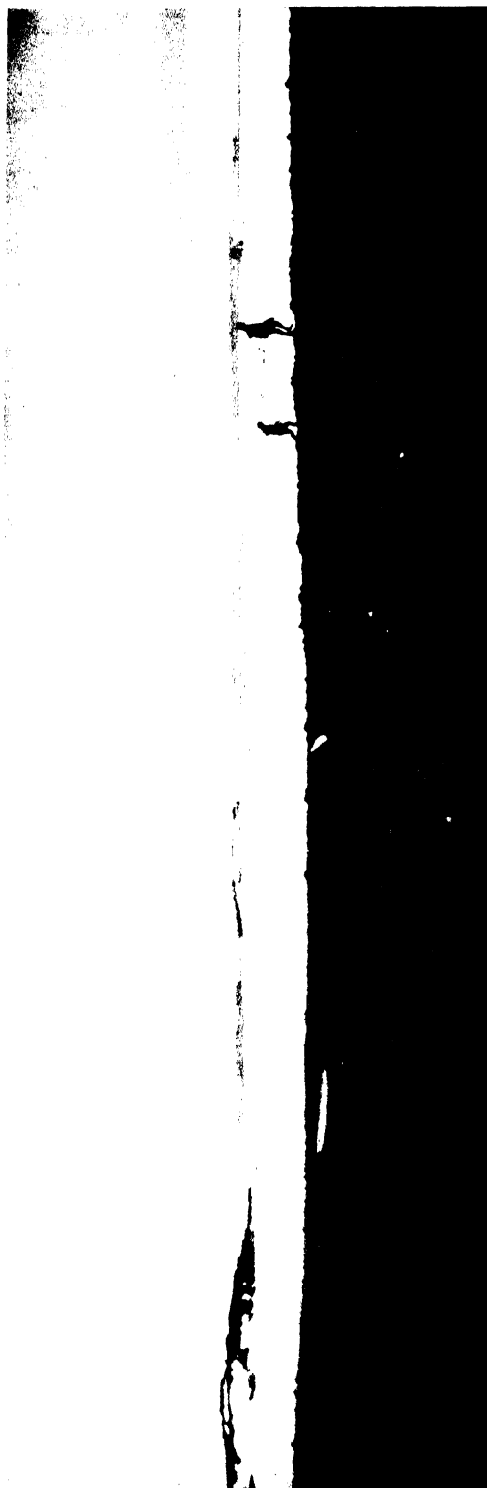
The original detailed data upon which this paper is based, together with a number of other unpublished observations, are being deposited in the Polar Institute, at Cambridge, for the use of future investigators. We are convinced that, in the past, many valuable ecological observations have not been recorded permanently; simply because it was impossible at the time for the observer to appreciate their significance. The deposition of such apparently disjointed notes in the form of archives at some suitable place, would, we feel sure, eventually result in the formation of a mass of data of real use to anyone working on the subject afterwards.

It is a pleasure to acknowledge the great help and co-operation received from members of the expeditions, among whom we particularly wish to thank the leader, Mr George Binney, for giving every possible facility for ecological work; Dr T. G. Longstaff, Messrs J. D. Brown and F. A. Montague, for many invaluable field observations, especially on the birds, but also on other points; Messrs H. M. Clutterbuck and H. W. Florey for considerable assistance in making collections and field notes; Dr K. S. Sandford for help in innumerable ways, but particularly in connection with geology; and Mr R. A. Frazer, for notes made by him on sledging expeditions, both in North-East Land, and New Friesland. To Mr A. P. G. Michelmores we are indebted for the use of notes made by him in Storfjord while on the Cambridge Expedition of 1927.

It is only possible to work out the results of an ecological survey of this sort by enlisting the help of numerous specialists in the various groups of plants and animals studied. The work of identification is especially difficult and laborious in the case of collections from a remote place like Spitsbergen. We wish therefore to thank the following ladies and gentlemen for their generous assistance in this connection: ANIMAL GROUPS—Dr G. H. Carpenter (Collembola), Mr J. E. Collin and Mr F. W. Edwards (Diptera), Rev. J. E. Hull (Mites), Dr A. R. Jackson (Spiders), Dr J. Stephenson (Oligochaete Worms), and Mr F. Laing (Aphids); PLANT GROUPS—Dr N. Carter (Fresh-water Algae), Miss M. M. Duke (Marine Algae), Mr H. N. Dixon (Mosses), Mr R. Paulson (Lichens), Miss E. M. Wakefield (Fungi), and Mr A. J. Wilmott (Phanerogams and Pteridophytes). Separate systematic papers have in many



Phot. A. V. T. Koudin
 Phot. 1. A retreating ice-sheet. The photograph, taken at Cape Torell, on the south coast of North-East Land, shows the narrow strip of land left by the retreating ice. The sea in the foreground is unusually free from floating ice.



Phot. E. J. Kelly
 Phot. 2. The barren Zone, as illustrated by a small dolerite island close to Von Otter Island, in Hinlopen Strait. The vegetation is very poor; in the background can be seen the ice-pack, and on the land several bits of driftwood from Siberia.

cases already been published by them. For permission to publish various photographs we tender our thanks to Dr T. G. Longstaff, Messrs J. D. Brown, F. G. Binney, A. N. T. Rankin, E. J. Relf, G. Summers, F. Tymms, and J. Walton,

Finally, we are greatly indebted to Prof. E. B. Poulton for kind assistance in dealing with animal material, and to Mr A. D. Cotton for permission to use the library and collections at the Royal Botanic Gardens, Kew.

At first sight, the plant and animal communities of Spitsbergen seem to vary from place to place in a most bewildering manner; but further analysis shows that these local differences can be related, in almost every case, to the interaction of four independent environmental factors, viz. climate, underlying rock, manuring by sea-birds, and water-supply. Owing to the marked differences of climate between the north-eastern and the western regions, and the great variety of rock-types (which include dolerite, gneiss, granite, shales, sandstones, and limestones, together with raised beaches and boulder-clay), it is possible to find almost every combination of climate and rock, each with its own effect on the life which it supports. Since some of these combinations are found over larger areas than others, we propose to deal with these more fully. We have therefore selected three important and well-marked types of country which illustrate three kinds of climate, but are each on a different type of rock. These are as follows:

(a) Dolerite areas in Hinlopen Strait, with a very severe climate (Section III).

(b) Reindeer Peninsula (Liefde Bay) consisting of shaly sandstones, in a more favourable climate (Section IV).

(c) The hinterland of Aldert Dirkses Bay (Wijde Bay), composed of gneiss and granite, enjoying a still more favourable climate (Section V).

The third factor, manuring by sea-birds, cuts right across the other two, producing its own characteristic communities; these are dealt with separately (Section VI).

Looked at from another point of view, the three areas can be considered as representing three different stages in the occupation of land recently exposed by a retreating ice-sheet (see Pl. XXIV, Phot. 1, and Pl. XXV, Phot. 3). The earliest stages in the series, however, are the communities living on snow and floating ice, which we propose to describe first.

II. COMMUNITIES OF ICE-PACK AND SNOW.

(a) ANIMALS OF THE ICE-PACK.

The polar current, setting across from Bering Straits to the Greenland and Barent's Seas, strikes Spitsbergen on the north and east coasts, carrying with it large amounts of more or less loose pack-ice (Pl. XXVI, Phot. 6). In winter the archipelago is completely surrounded by this ice, but in summer only the northern and eastern parts are affected. The movements of the ice are very

capricious, depending upon the winds and currents, and for this reason North-East Land has only occasionally been circumnavigated. In the summer of 1923, our party spent some time exploring among the pack-ice at the south end of Hinlopen Strait and, later, on the north coast of North-East Land, and there were many opportunities of studying the animals which live on the ice-floes. These are three in number:

The Great Bearded Seal or Storkobbe (*Erignathus barbatus*).

The Polar Bear (*Ursus arctos*).

The Ivory Gull (*Pagophila eburnea*).

The seals are large animals about 8 ft. long, and dark greyish brown in colour, and they subsist on marine animals such as fish and crustacea. While digesting this food they lie out sluggishly on the edges of thick ice-floes, and they are then hunted by bears, which try to creep up behind them and kill them. We watched one bear stalking a seal, which, however, slipped away before it was caught; and on one occasion the claw marks of a bear were found on the skin of a seal which was shot, while the stomachs of several bears were found to contain seal skin. The Storkobbe must be the chief food of the Polar Bear in summer, in this region. Only two other species of seal occur round Spitsbergen, viz. the Ring-seal (*Phoca foetida*) and the Greenland Seal (*Phoca groenlandica*); the latter is uncommon near the coast, but is occasionally seen in parties travelling along at sea (as on July 28th, 1924, outside Liefde Bay), while the former is not important as bear-food in summer, for the reasons given below. The Ring-seal is much smaller than the Storkobbe, and is found very commonly all round the coasts of Spitsbergen, both in the regions of ice-pack, and in the warmer regions of the fjords. In early spring the seals bring forth their young ones on the thin bay-ice, which still persists at that time from the previous winter, and in the colder localities (as on the north coast of North-East Land), they may still be found on such persistent bay-ice in August. But in most places the Ring-seals appear to lead a completely aquatic existence in summer; in Liefde Bay, for instance, where there is no ice in summer, the seals live entirely in the water in July and August, feeding upon planktonic crustacea (*Mysis*) in company with Little Auks (*Plutus alle*), and never coming to land. It seems certain therefore that the Ring-seals cannot be eaten by bears in summer to any large extent, since the latter do not hunt them in the water, and are probably unable to venture on to the thin bay-ice. The bears must therefore feed almost exclusively on Storkobbes in summer, but may catch Ring-seals also in winter.

The Ivory Gull is to the Polar Bear what the jackal is to the African lion: it subsists almost entirely on the carcasses of seals left by bears, and to a minor extent, nowadays, on those left by the Norwegian sealers. This gull is a very remarkable bird, for it has become so much attached to the ice-pack that it practically never goes on the water at all, showing extreme reluctance towards alighting on the surface, even to obtain food. In this way it is more like a

*Phot. F. Tynnis*

Phot. 3. An aerial photograph of the coast of North-East Land near Lady Franklin Bay. The solid white part is the ice-sheet which has retreated, leaving a narrow strip of very barren land. The fluffy white parts are clouds, while the black part dotted with white, in the lower half of the photograph, is the sea, containing small floating icebergs from the glacier seen on the extreme right-hand side.

*Phot. J. P. Brown*

Phot. 4. Mandt's Black Guillemot (*Uria grylle mandtii*) at the entrance of its nesting place on a dolerite cliff on the Foster Islands, Hinlopen Strait. A number of crustaceous rock lichens, produced by the manuring of the birds, can be seen covering the rocks.

land-bird than a sea-bird. It was sometimes seen drinking fresh water formed by the melting snow on the surface of the ice-floes. The greatest number of Ivory Gulls was observed at Ulve Bay, where seals and bears were also numerous. It may be noted that the Ivory Gull is pure white in colour, all over its body, except for a yellow beak and black legs. This coloration makes it very difficult to see when it is sitting motionless among the ice-floes, since the light falls from above and is also reflected from below, producing no shadows, and therefore making the bird seem to have no solidity. These facts might give some justification for regarding the Ivory Gull as a bird which is beautifully adapted to escape enemies amidst its polar surroundings, were it not for the fact that it has no enemies at all in summer, when the effect we are speaking of is produced. And yet it differs from all the common marine gulls of temperate regions in having no grey or black on its plumage. It is just possible that the inconspicuousness is of service to it in winter, when it may have to compete with Arctic Foxes (*Canis lagopus*), which at that time come out on to the sea-ice and follow the bears for their leavings. But it is dark in winter, except for periodic moonlight, and it seems likely that the coloration of the Ivory Gull falls into the same class as that of the Arctic Fox, which turns white in winter, but has an equally successful variety living with it which turns *black* in winter (9, p. 182); and the two species of Lemming found in arctic Siberia and America (but not in Spitsbergen), one of which (*Dicrostonyx*) turns white in winter while the other (*Lemmus*) does not, both however living together *under the snow* at this time. Finally the Polar Bear, theoretically white, is only so in winter; in summer its fur is stained a dirty yellowish colour by the diatoms which are so numerous in the sea-water. There is no doubt that polar animals do tend to be white or to turn white in their white surroundings; there seems equally little doubt that the reason for this is not always the obvious one of concealment from enemies or prey, while at the same time there are several cases in which the colour does seem to be of real use to its owners (e.g. Snowy Owl and Ptarmigan).

The Storkobbe, Polar Bear, and Ivory Gull form an interesting and clear-cut community, to which in recent years has been added another member—Man. Norwegian sealers now take a heavy toll of seals and bears every summer, and the effect of this upon the numbers of the animals has been dealt with by one of us elsewhere (9, p. 121).

The Walrus (*Trichechus rosmarus*) occurs still in some numbers in the more inaccessible regions where the ice-pack makes approach difficult, and it was met with by us at Ulve Bay in 1923; but it is not particularly an ice-pack animal, although it does lie out on thick floes at times. It breeds on land, and often comes there in summer, and it feeds on the mussels (*Mya truncata*) and other animals which come in shallow waters. It is not attacked normally by the Polar Bear, and so has no part in the community we have been describing.

(b) THE FAUNA AND FLORA OF SNOW.

(a) Red snow.

Bruce (4, p. 81) says, "I have seen acres of ice and snow red with this alga [*Sphaerella nivalis*] in Prince Charles Foreland, and other parts of Spitsbergen, as well as in Novaya Zemlya and Franz Josef Land." However, the Oxford parties very seldom encountered genuine red snow during the three summers they were in Spitsbergen. It was hardly ever seen by the three parties which sledged over the ice-cap of North-East Land in 1924. R. A. Frazer and K. S. Sandford obtained a specimen of red snow from the snow-plug of a crevasse about 1100 feet above sea-level and 15 miles inland (Amen Camp); but this patch (which proved to be the resting stages of *S. nivalis*) was the only one seen by them during several weeks' sledging. The rarity of the alga on North-East Land is perhaps not surprising when we take into consideration the comparatively low altitude of the ice-cap, which nowhere rises above 2400 ft. There is, accordingly, a very sudden and tremendous melting of the surface snow for a few weeks in the summer—so enormous is the amount of water produced that the sea-water at the mouth of Wahlenberg Bay (a fjord about 40 miles long) was found to be practically *fresh* in the middle of August 1924. The rarity of red snow on North-East Land is therefore due to the rarity of permanent surface snow in summer, while most of the water produced by melting of the snow runs down into the sea.

In the interior of West Spitsbergen the conditions are rather different, most of the areas of inland ice and snow rising above 3000 ft. (900 m.), while several mountains rise above 5000 ft. (1500 m.). In consequence of this, there are large areas of permanent snow in summer, and the Oxford party which sledged over New Friesland in 1923 several times met with large patches of red snow. N. E. Odell and R. A. Frazer reported a great deal of it below Castle Crags at the head of Bear Bay, where there were also rich flower slopes below the cliffs, upon which was a colony of nesting fulmar petrels. They also collected a sample of red snow from Mount Tchernichev.

The differences between North-East Land and New Friesland, due to their different heights above sea-level, are reflected in the summer sledging conditions, which are appallingly wet in the former, but comparatively hard and dry in the latter.

It appears, however, that *Sphaerella nivalis* in Spitsbergen is not confined to permanent snow, for Bruce says (4, p. 83) that the dried-up shallow ponds and pools found in late summer often have a dark reddish scum covering the bottom, and that this consists mainly of *S. nivalis*. The members of Parry's expedition in 1827 observed the same thing (24, p. 218). Bruce adds that this phenomenon is especially common where the water-supply comes from bird-cliffs. We noticed that the shingle beach at Bruce City (head of Klaas Billen



Phot. C. S. Elton

Phot. 5. The north coast of North-East Land, east of Cape Platen. Granite rocks, under the most severe conditions of climate. This region is usually cold and foggy in the summer.



Phot. T. G. Longstaff

Phot. 6. Drift-ice in Hinlopen Strait. The ice-floes support a special fauna of their own, including seals, bears and Ivory Gulls.

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Face p. 199

Bay) was covered in places with a reddish scum which consisted of this alga; at this time all the snow had disappeared.

It appears, then, that in Spitsbergen *Sphaerella nivalis* maintains itself in two quite different ways: either by living on permanent snow in places over 3000 ft. (900 m.), or occurring on snow early in the season and continuing to live in pools, etc., after the snow has turned into water. It is possible that the red snow seen so commonly by Bruce occurred in the latter class of habitat, as he was there earlier in the season than we were.

A good deal remains to be discovered about the methods of growth and dispersal of this alga. We may note that Parry found it growing very commonly on the frozen sea-ice, and he remarked that the sledges left red tracks behind them in the snow (24, p. 109).

Little is known about the animal inhabitants of red snow in Spitsbergen, but a nematode worm (*Aphelenchus nivalis*) has been recorded by Aurivillius (1a) from this habitat.

We have pointed out previously (29, p. 231) that the remains of crustacea forming the droppings of Little Auks sometimes look like red snow. Bruce also comments on this, but adds that he found red snow below bird-cliffs to contain *S. nivalis* as well as droppings. It is obvious that specimens are desirable to confirm records of red snow in such places.

(b) Springtails on snow.

There are certain species of springtails (Collembola) which occur on snow in alpine countries. Among these is *Agrenia bidenticulata*, which is the only species we have found in such places in Spitsbergen. It was noticed on snow-drifts in early July on Prince Charles Foreland, and also on hard banks of snow in a sheltered gully at Cape Roos, Liefde Bay, in July. In both cases the insects were fairly numerous and quite active. At Cape Roos there was a good deal of wind-blown debris contained dead *Salix* leaves, etc., on the snow, and presumably the springtails obtain their food there. There is always a great deal of dust on such snow-patches, some of which is sure to be of vegetable origin. *A. bidenticulata* comes also quite frequently in other habitats.

(c) Worms in the ice-foot.

Large numbers of the common maritime and intertidal oligochaete worm, *Lumbricillus aegialites*, were found living in the snow which covered the ice-foot on the Canard Islands in Liefde Bay in July 1924. The ice-foot is the remains of the frozen ice of the winter, which still hangs on to the shore, and is covered with snow. At this time it had nearly disappeared, and there were only 2 in. (5 cm.) of ice left between the snow above and the sea-weed lying at the drift-line below. The worms were living both in the snow and in the sea-weed; they were very active, and were forming an important article of food

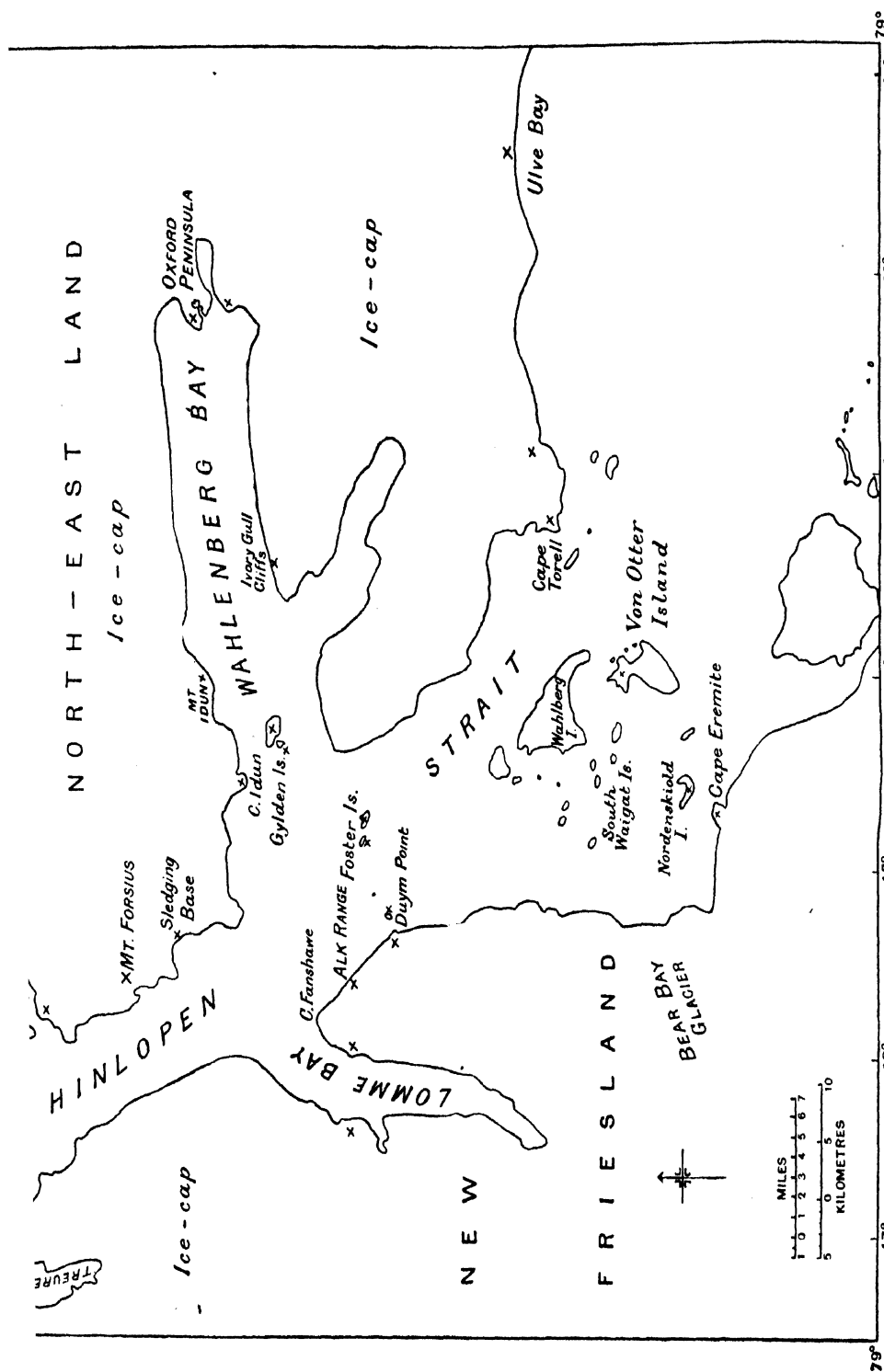


FIG. 1. Sketch-map of Hinlopen Strait and Wahlenberg Bay, showing places where ecological work was done (marked with x). (Mainly from the map of the Swedish Arc of Meridian Expedition in 1899-1902; Wahlenberg Bay, and some details, from Oxford Expedition surveys of 1923 and 1924.)

for Purple Sandpipers (*Erolia m. maritima*). In the previous year we had seen Sandpipers and Turnstones (*Arenaria i. interpres*) feeding on similar stretches of the ice-foot on the mainland of Reindeer Peninsula, doubtless in search of the same worm food. These worms must have been able to withstand freezing for long periods; it is worth noting in this connection that another small worm, *Enchytraeus crymodes*, found in salt-marsh mosses at Bruce City, was found to withstand freezing for some time in a glass tube (28, p. 1110).

III. NORTH-EAST LAND AND HINLOPEN STRAIT.

North-East Land, which is an island about the size of Wales, lies, as its name implies, to the north-east of the main island of Spitsbergen (which is called West Spitsbergen). Owing to its distance from the Gulf Stream drift and the fact that the northern, eastern, and southern sides are washed by a polar current, which carries pack-ice to its shores in summer, it is subjected to much more severe climatic conditions than the rest of Spitsbergen (Pl. XXVI, Phot. 5). A large ice-cap occupies the centre of the island, leaving an ice-free zone of variable width around the coast; owing to the prevailing low temperature and fog, frost action is very severe in this zone, and consequently the rocks, with the exception of extremely hard ones such as dolerite, are rapidly split up into small stones and finally mud. The country is everywhere very dreary, the ground being covered with rocky debris; while the vegetation, with one exception, is of a very stunted nature. Only in the neighbourhood of bird-cliffs, and in special localities at the heads of the longer fjords are plants at all well developed. In some places, as at Murchison Bay, it is possible to walk for miles over the frost-shattered surface without seeing more than an occasional tuft of poppies (*Papaver radicum*); these form the exception noted above, for they are very common, and often form tufts of unusual size, covered with flowers, even in the most barren districts such as Ulve Bay and Cape Torell.

Owing to the fact that it was impossible to visit all the ice-free areas personally, we are unable to describe the vegetation of the whole in any detail. However, the islands, and parts of the coast of Hinlopen Strait (on the New Friesland side) are subjected to the same severe climate and here the plants were studied more carefully. The vegetation occurring on the igneous rock dolerite is described in detail, to give an idea of the plant communities found in this, the most barren and inhospitable part of the archipelago. (The following dolerite areas were visited: the Alkrange, Duym Point, Cape Eremite, Foster Islands, South Waigat Islands (including Von Otter Island and Nordenskiöld Island), Gylden Islands, Sledging Base, and Cape Idun. These are shown in detail on the map in Fig. 1.)

(a) THE FLORA OF THE DOLERITE AREAS.

Intrusions of dolerite, a basic igneous rock resembling basalt, are found mainly along Hinlopen Strait, most of the islands being composed of this rock, with raised beaches overlying it here and there. On the south side of the strait, there are two important outcrops at the Alkrange and Cape Eremite, while on the north side, Hyperite Point and Cape Idun are the chief areas, although there are also outcrops in Wahlenberg Bay and at Cape Torell. These dolerite areas occur in a region which is characterised by a very severe climate, and as a result the vegetation is exceedingly poor; in fact, the dolerite in Hinlopen Strait is one of the most barren types of soil in Spitsbergen, although where it occurs in more favourable situations (as at Anser Islands, in Icefjord) it may support a luxuriant flora. The photograph in Pl. XXIV, Phot. 2, gives a good idea of the scenery of the barren dolerite. Often the only animal life to be seen consists of a few chironomid flies, a snow bunting, or an occasional skua.

On the dolerite outcrops a well-marked succession may be traced from the bare rock to various semi-closed or, rarely, closed communities.

(a) Rock surface.

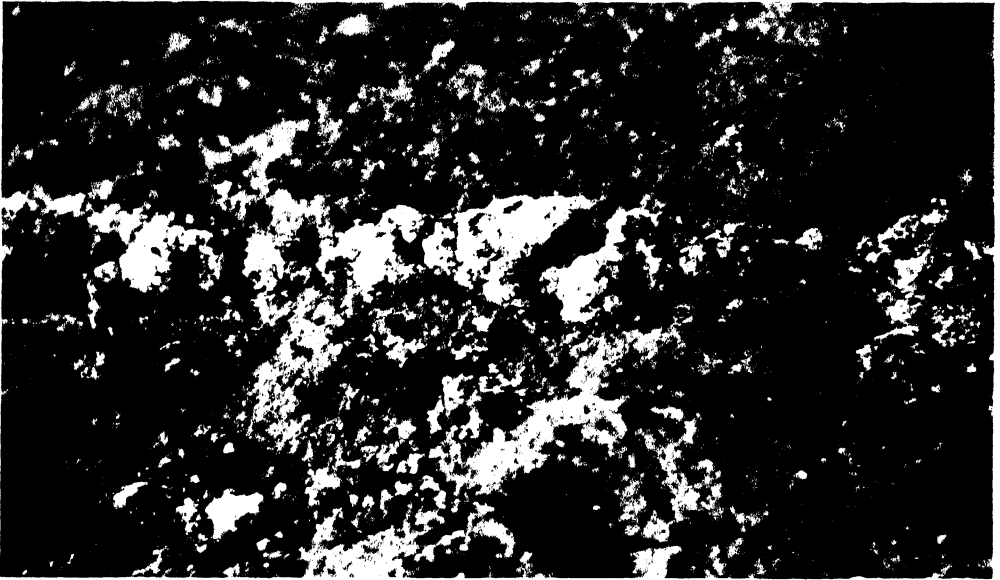
The vegetation of the dolerite rock surface consists almost entirely of lichens, of which the rusty red *Lecidea dicksonii* and the black *Parmelia pubescens*, together with several species of *Gyrophora*, are the most characteristic. A more complete list follows, but doubtless many less frequent species occur:

| | |
|--|--|
| <i>Acarospora lesdainii</i> | <i>L. sordida</i> var. <i>inflexa</i> |
| <i>A. chlorophana</i> | <i>Lecanora tartarea</i> var. <i>frigida</i> |
| <i>Alectoria jubata</i> var. <i>chalybeiformis</i> | <i>Lecidea confluens</i> |
| <i>Buellia disciformis</i> var. <i>saxicola</i> | <i>L. dicksonii</i> |
| <i>Caloplaca jungermanniae</i> (on moss) | <i>L. pantherina</i> |
| <i>Candelariella vitellina</i> | <i>Pannaria hookeri</i> |
| <i>Gyrophora cylindrica</i> | <i>Parmelia pubescens</i> |
| <i>G. erosa</i> | <i>Rhizocarpon geographicum</i> |
| <i>G. hyperborea</i> | <i>Usnea sulphurea</i> |
| <i>G. proboscidea</i> | <i>Xanthoria parietina</i> vars. <i>aureola</i> and <i>ectanea</i> |
| <i>Lecanora polytropa</i> | <i>X. lychnaea</i> |

Many of these species occur also on quite different rocks, but the association as a whole is characteristic of the dolerite. *Andreaea papillosa* is a rare though typical moss of the rock surfaces.

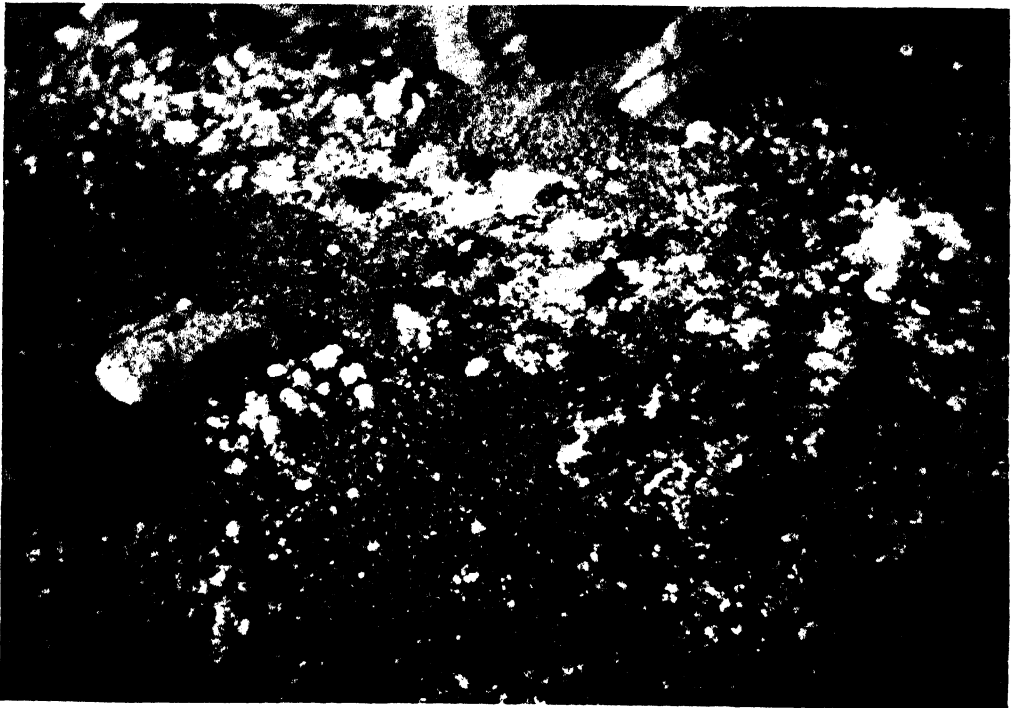
(b) Rock crevices.

With the weathering of the rock, mainly through frost-action, crevices are produced which immediately offer habitats for plants unable to grow on the rock surface itself. The crustaceous lichens are replaced by foliose and fruticose forms (Pl. XXVII, Phot. 7), and with them occur a number of



Phot. C. S. Elton

Phot. 7. Succession on dolerite on the Gylden Islands, Hinlopen Strait. The photograph shows rock-lichens on the surface of the rock, and, across the middle, a crevice being colonised by other lichens, such as *Stereocaulon alpinum*, and *Lecanora tartarea* var. *frigida*.



Phot. C. S. Elton

Phot. 8. Succession on dolerite on the Gylden Islands in Hinlopen Strait. The dry soil produced by the weathering of dolerite is being invaded by lichens, chiefly *Stereocaulon alpinum*.

*Phot. C. S. Elton*

Phot. 9. Succession on dolerite on the Gylden Islands, Hinlopen Strait. A further stage in invasion of the soil, which has become covered by lichens, together with a few mosses. The species concerned are listed on p. 203.

*Phot. C. S. Elton*

Phot. 10. Succession on dolerite on the Gylden Islands, Hinlopen Strait. Final stage reached in this climate, consisting of a mat of Arctic Willow, *Salix polaris*, which has replaced the lichen carpet, of which the remains can be seen at the edges.

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mosses. The following list was made at the Foster Islands, and can be taken as typical of the dolerite areas in Hinlopen Strait.

LICHENS.

| | |
|---|--|
| <i>Alectoria ochroleuca</i> | <i>Collema</i> sp. |
| <i>Bilimbia subfuscula</i> | <i>Gyrophora erosa</i> |
| <i>Caloplaca cinnamomea</i> | <i>G. hyperborea</i> |
| <i>C. jungermanniae</i> var. <i>subolivacea</i> | <i>Lecanora tartarea</i> var. <i>frigida</i> |
| <i>Cetraria hiascens</i> | <i>L. upsaliensis</i> |
| <i>C. islandica</i> | <i>Lecidea limosa</i> |
| <i>Cladonia pyxidata</i> and var. <i>neglecta</i> | <i>Rinodina turfacea</i> |
| <i>C. furcata</i> var. <i>palamaea</i> | |

MOSSES.

| | |
|---|---------------------|
| <i>Hypnum uncinatum</i> | <i>Webera cruda</i> |
| <i>Polytrichum alpinum</i> var. <i>septentrionale</i> | <i>W. cucullata</i> |

Other mosses occurring in such places are *Bartramia ithyphylla*, *Dicranoweisia crispula*, *Grimmia apocarpa*, and *Swartzia montana*. As the cracks become deeper and wider and filled with soil, more and more species invade them and lichen heath tends to be slowly established, by the gradual fusion of the different foci of invasion. But at most places, such as the Gylden Islands and Cape Eremit, the rocks weather away faster than they are invaded, so that a rather dry, loose, crumbly soil is produced. This is colonised primarily by a few species of lichens, of which *Stereocaulon alpinum* is the most prominent, others being *Lecanora tartarea* var. *frigida* and *Rinodina turfacea* (Pl. XXVII, Phot. 8). These are followed by other lichens and mosses, together with scattered phanerogams, and lichen or moss heath is eventually produced (Pl. XXVIII, Phot. 9).

(c) Lichen or moss heath.

It is almost impossible to draw any line between the communities dominated by lichens and mosses respectively, and indeed often the groups appear in equal quantities. The composite community occupies large areas on ground between weathering outcrops and boulders, and varies from more or less open communities in an early stage of succession, to dense luxuriant carpets of vegetation. A remarkably luxuriant example of lichen heath is to be found at Duym Point, the sledging base of the party which crossed New Friesland in 1923.

Phanerogams occur in varying amount in the moss-lichen heath, but are always subordinate to the cryptogams. Of the lichens, *Cetraria islandica*, *C. hiascens*, *C. aculeata*, *C. nivalis*, *Stereocaulon alpinum*, and *Lecanora tartarea* var. *frigida*, are the most important, while *Rhacomitrium lanuginosum*, *Hypnum uncinatum*, and *Polytrichum alpinum* are the chief mosses. The most characteristic species of higher plants are *Luzula confusa*, which often appears early in the succession, *Papaver radicum*, *Salix polaris*, and *Saxifraga oppositifolia*. A general list of the flora of the moss-lichen heath, compiled from many different localities, is given below, the phanerogams in particular

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seem to vary considerably in different places, and while this may be due to different edaphic conditions, it is also probably due to chance dispersal, since many of the localities studied were islands.

PHANEROGAMS.

| | | |
|-------------------------------|------------------------------|------|
| <i>Alopecurus alpinus</i> | <i>Polygonum viviparum</i> | v.l. |
| <i>Cardamine bellidifolia</i> | <i>Potentilla emarginata</i> | |
| <i>Catabrosa algida</i> | <i>Ranunculus sulphureus</i> | |
| <i>Cerastium alpinum</i> | <i>Salix polaris</i> | |
| <i>C. regelii</i> | <i>Saxifraga caespitosa</i> | |
| <i>Cochlearia officinalis</i> | <i>S. cernua</i> | |
| <i>Draba lactea</i> | <i>S. flagellaris</i> | |
| <i>D. oblongata</i> | <i>S. nivalis</i> | |
| <i>Luzula confusa</i> | <i>S. oppositifolia</i> | |
| <i>Oxyria digyna</i> | <i>S. rivularis</i> | |
| <i>Papaver radiculatum</i> | <i>Stellaria longipes</i> | |

MOSESSES.

| | |
|---|--|
| <i>Bartramia ithyphylla</i> | <i>Hypnum uncinatum</i> |
| <i>Bryum crispulum</i> | <i>H. vaucheri</i> |
| <i>Cynodontium virens</i> and var. <i>arcticum</i> | <i>Orthothecium chryseum</i> |
| <i>Dicranoweisia crispula</i> | <i>O. strictum</i> |
| <i>Dicranum bonjeani</i> var. <i>juniperifolium</i> | <i>Polytrichum alpinum</i> |
| <i>D. elongatum</i> | <i>Racomitrium canescens</i> |
| <i>Ditrichum flexicaule</i> var. <i>densum</i> | <i>R. lanuginosum</i> |
| <i>Encalypta rhabdocarpa</i> | <i>Swartzia montana</i> var. <i>brevifolia</i> |
| <i>Fissidens osmundoides</i> | <i>Timmia austriaca</i> |
| <i>Grimmia apocarpa</i> | <i>Tortula ruralis</i> |
| <i>Hypnum polare</i> | <i>Webera cucullata</i> |
| <i>H. turgescens</i> | <i>W. cruda</i> |

LICHENS.

| | |
|--|--|
| <i>Alectoria ochroleuca</i> | <i>Cetraria nivalis</i> |
| <i>Biatorina cumulata</i> | <i>Lecanora tartarea</i> var. <i>frigida</i> |
| <i>Buellia disciformis</i> var. <i>insignis</i> | <i>L. upsaliensis</i> |
| <i>Caloplaca cinnamomea</i> var. <i>hypnophylla</i> | <i>Lecidea alpestris</i> |
| <i>C. jungermanniae</i> var. <i>subolivacea</i> | <i>Parmelia omphalodes</i> |
| <i>C. stillicidiorum</i> | <i>P. pubescens</i> |
| <i>Cladonia cariosa</i> | <i>Pertusaria dactylina</i> |
| <i>C. coccifera</i> | <i>Physcia pulverulenta</i> |
| <i>C. degenerans</i> | <i>Psoroma hypnorum</i> |
| <i>C. furcata</i> var. <i>palamaca</i> | <i>Rinodina turfacea</i> |
| <i>C. f.</i> var. <i>recurva</i> | <i>Solorina crocea</i> |
| <i>C. pyxidata</i> and var. <i>chlorophaea</i> f. <i>lepidophora</i> | <i>Sphaerophorus globosus</i> |
| <i>Cerania vermicularis</i> | <i>Stereocaulon alpinum</i> |
| <i>Cetraria aculeata</i> | <i>S. denudatum</i> var. <i>pulvinatum</i> |
| <i>C. cucullata</i> | <i>S. evolutum</i> |
| <i>C. hepatizon</i> | <i>S. paschale</i> |
| <i>C. hiascens</i> | <i>S. tomentosum</i> |
| <i>C. islandica</i> and var. <i>tenuifolia</i> | <i>Xanthoria lychnaea</i> |
| | <i>X. parietina</i> var. <i>ectanca</i> |

Of the mosses, most of the species are those preferring dry habitats; but some occur in damper places, while in certain regions damp sub-communities may be found making a transition to moss-bogs, *Salix polaris* being sometimes important in such places (see 29, p. 224). Among the lichens, some grow on the smaller stones imbedded in the moss-carpet, but most of the species are terrestrial. The extraordinary richness of the lichen flora is evident from the lists. Although the horns and dung of reindeer, which feed on such lichens and mosses, were found at Duym Point and on the Gylden Islands, no

signs whatsoever of them were noticed at the very inhospitable localities farther down Hinlopen Strait, in spite of the moss-lichen heaths occurring there. It is possible that the two places mentioned are visited only on migration, since they lie on the route from the comparatively fertile regions at the head of Wahlenberg Bay to those inside Lomme Bay.

The lichen or moss heath seems to be the climax community on dolerite in this region, although there is a suggestion in places of a transition to a very primitive type of dwarf-shrub heath, dominated by *Salix polaris*, which occurs in large, almost pure patches locally (Pl. XXVIII, Phot. 10). *Dryas octopetala*, however, is completely absent.

Eider Ducks (*Somateria mollissima borealis*) often find favourable nesting places among the rocky outcrops of the islands (see Hermannsen I. 29, p. 281), and here the lichen heath is replaced by phanerogams, especially grasses. The replacement is more complete with increase in the manuring, until the conditions occurring on bird-islands (see under Nitrophilous Communities) are reached, and a more or less complete grass-turf is found. *Catabrosa algida* and *Carex nardina* are the chief plants, while the presence of *Cochlearia officinalis*, *Cerastium alpinum*, *Saxifraga cernua* and *S. rivularis*, in increased quantity, connects these communities with true nitrophilous ones, to which some of these islands might be referred. "Skua hummocks," i.e. the grassy knolls produced by the nesting and watching Skuas, and bird-cliffs, occur in various places; these are dealt with under Nitrophilous Communities.

(d) Bogs.

Areas where the drainage is imperfect, generally associated with pools, occur on all the dolerite areas, and support the usual type of moss-bog community found in Spitsbergen. Eider Ducks and other aquatic birds frequent such places, with the result that the community is rarely free from the effects of manuring; Red-throated Divers (*Colymbus stellatus*) nest in the moss zone at the edge of tarns, and make their nests out of the mosses. We have not sufficient data to allow us to differentiate between the manured and unmanured bogs. The most characteristic phanerogam is *Saxifraga rivularis*, while others are *Ranunculus hyperboreus* (in the wettest parts) and various grasses.

Of the bryophytes, *Bryum crispulum*, *Hypnum brevifolium*, *H. sarmentosum*, *H. stellatum*, *H. uncinatum* and *H. zemliae*, have been noticed. It is significant that the extreme damp-loving or semi-aquatic species, such as *Hypnum cordifolium* and *H. giganteum*, do not figure in the lists, this being due to the fact that the trampling of the birds has destroyed the plants in the wetter parts. A few lichens are associated with the mosses, e.g. *Cetraria hiascens*, *Lecanora limosa*, *L. tartarea* var. *frigida*, and *Caloplaca cinnamomea*; but generally they are of little importance.

(e) **Raised beaches.**

It will be fitting at this point to describe the raised beaches which occur on the dolerite islands in Hinlopen Strait, and also on the adjacent mainland. These beaches may contain fragments of dolerite itself, but are mainly composed of other and very diverse kinds of rocks, such as limestones, quartzites and shales. The community on these beaches is usually a fjaeldmark of the normal type, in which the plant covering is never closed, and consists mainly of phanerogams. Many species of lichens and mosses may be present, but they never play an important rôle in the community. In places the stones of the beaches have become mixed with mud, either from their own disintegration, or brought down from the slopes above, and in such places polygonal soils of various types are found, chiefly stone-polygons in a late stage of development, the borders having almost disappeared (see 8). On the shale and limestone fragments the following lichens have been found, and although many of these occur on the dolerite, yet the rarity of *Lecidea dicksonii*, which is so characteristic of the latter rock, is significant, and the absence of the wealth of *Gyrophora* species found on dolerite is also interesting:

| | |
|------------------------|--|
| <i>Buellia coniops</i> | <i>Lecidea arctica</i> |
| <i>Gyrophora erosa</i> | <i>L. confluens</i> and var. <i>oxydata</i> |
| <i>Lecanora alpina</i> | <i>L. pantherina</i> |
| <i>L. lesleyana</i> | <i>Parmelia pubescens</i> |
| <i>L. nikrapensis</i> | <i>Rhizocarpon geographicum</i> |
| <i>L. polytropa</i> | <i>Xanthoria parietina</i> var. <i>ectanea</i> |

This list is very incomplete, but gives an idea of the lichen flora of these non-dolerite areas.

Where the soil is not polygonally differentiated, the distribution of the phanerogams, etc., is more or less regular, but in polygon areas the rocky edges are often devoid of plants other than the lichens given above.

The phanerogams are a mixed assemblage with no particular dominant, but *Papaver radiculatum* and *Saxifraga oppositifolia* are the most abundant and striking species. A list embracing four localities is given below in order to show local variation, the localities being (1) the Gylden Islands, (2) Von Otter Island (South Waigat Islands), (3) Cape Eremite, (4) Ulve Bay. It should be mentioned that there is little dolerite at Ulve Bay, the rock being limestone and sandstone of Carboniferous age, but the raised beaches there are so similar to those in Hinlopen Strait that it was considered of value to include them in the account. At (2) and (3) polygon areas are abundant.

The species marked with an asterisk on p. 207 were found in a damp fjaeldmark society which was not noticed at the other three localities. The places are arranged in order of richness of the flora, and it will be seen that the raised beaches at Ulve Bay are much poorer in species than the other places; while the Gylden Islands, which are still less affected by the ice-pack in summer, possess an even richer fjaeldmark flora. It is thus clear that the climatic

gradient in the flora dealt with more fully on p. 252 is exhibited not only in a general manner, but may also be traced in a given community occurring within the range of one climatic zone. In other words the "zones" employed by us are to some extent arbitrary, and merely mark the arrival of certain important dominants into what is really a gradual change in the vegetation.

| | Gylden Islands | Von Otter Island | Cape Eremit | Ulve Bay |
|--|-------------------|---------------------|----------------|----------|
| <i>Alsine rubella</i> | × | — | — | — |
| <i>Cardamine bellidifolia</i> | × | × | × | — |
| <i>Carex</i> sp. | × | × | — | — |
| <i>Catabrosa algida</i> | × | × | — | × |
| <i>Cerastium alpinum</i> | × | × | — | × |
| <i>C. regelii</i> | × | × | × | — |
| <i>Cochlearia arctica</i> and/or <i>groenlandica</i> | × | × | × | × |
| <i>Draba lactea</i> | × | × | × | — |
| <i>D. oblongata</i> | × | × | × | × |
| <i>D. pauciflora</i> | × | — | — | — |
| <i>Glyceria angustata</i> | × | — | — | — |
| <i>Luzula confusa</i> | — | × | — | — |
| <i>Melandryum apetalum</i> | × | — | — | — |
| * <i>Oxyria digyna</i> | — | — | (×) | — |
| <i>Papaver radicatum</i> | × | × | × ab. | × ab. |
| <i>Poa abbreviata</i> f. <i>pallida</i> | × | — | — | — |
| <i>Potentilla emarginata</i> | × | — | — | — |
| * <i>Ranunculus sulphureus</i> | — | — | (×) | — |
| * <i>Salix polaris</i> | — | — | (× ab.) | — |
| <i>Saxifraga caespitosa</i> | × | ? × | × | × |
| <i>S. cernua</i> | × | × | × | × |
| <i>S. nivalis</i> | × | × | × | — |
| <i>S. oppositifolia</i> | × | × | × ab. | — |
| <i>S. rivularis</i> | — | × | — | — |
| <i>Stellaria humifusa</i> | × | — | — | — |
| <i>S. longipes</i> | × | × | × | × |
| | 21 | 16 | 11 (+3) | 8 |

(b) THE FAUNA OF NORTH-EAST LAND.

Since the nature of the rock does not usually act as a limiting factor to the distribution of animals in Spitsbergen, we are describing the fauna of North-East Land as a whole. Therefore, in addition to the dolerite areas already mentioned, this account includes other places such as North Cape, Extreme Hook, Isis Point, Ulve Bay, and Murchison Bay, the whole possessing a rather distinctive fauna as a result of the severe climate. Longstaff (18) has already pointed out that North-East Land forms a special area for birds, differing from the rest of Spitsbergen in the abundance of the Ivory Gull and in the absence of many species. Longstaff's observations have been extended and confirmed by Montague (21).

In order to provide some background for showing the extreme poorness of the North-East Land fauna, and also for comparison with other localities which we shall describe later on, a list is given below of all the animals which are known to live and breed normally in the dry-land associations of Spitsbergen (omitting Bear Island). This list includes the animals normally inhabiting moss-lichen heath, fjældmark, *Dryas* communities and

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Cassiope heath, but *not* those of the grass-turf produced by the manuring of birds. It does not include sea-birds which come to land to breed, since these play no part in the life of the land communities, apart from their indirect influence in manuring the soil. As far as the more barren parts of Spitsbergen are concerned, the list is probably fairly complete, since Zones 1 and 2 (see p. 252) have been worked out fairly well. Further work will doubtless reveal more species to add to this list, especially from the inner parts of the big fjords (Icefjord, Bell Sound and Wijde Bay). A number of insects (e.g. parasitic Hymenoptera) have been recorded from such places as Advent Bay and Green Harbour by Scandinavian scientists (3, 13) who worked there in the beginning and middle of the nineteenth century; but it has only been possible to use for this list the species whose habitats are definitely known. Therefore anything up to a dozen more species may be added to the list, when their habits are better known.

The species marked with an asterisk are either local or rare in Spitsbergen.

| | |
|---------------------------|--|
| MAMMALS: | Spitsbergen Reindeer (<i>Rangifer spitsbergensis</i>) Arctic Fox (<i>Canis lagopus</i>) |
| BIRDS: | Snow Bunting (<i>Plectrophenax n. nivalis</i>) Purple Sandpiper (<i>Erolia m. maritima</i>) Turnstone (<i>Arenaria i. interpres</i>) *Sanderling (<i>Crocethia alba</i>) Spitsbergen Ptarmigan (<i>Lagopus mutus hyperboreus</i>) Pink-footed Goose (<i>Anser brachyrhynchus</i>) |
| SPIDERS (Araneida): | * <i>Coryphaeus holmgrenii</i> <i>Erigone arctica</i> <i>E. psychrophila</i> * <i>E. tirolensis</i> <i>Hilaira glacialis</i> <i>Leptyphantus sobrius</i> * <i>Micaria eltonii</i> * <i>Micryphantus nigripes</i> <i>Typhochrestus spetsbergensis</i> |
| MITES (Acarina): | <i>Bdella decipiens</i> <i>B. groenlandica</i> <i>B. littoralis</i> <i>B. pallipes</i> * <i>Ceratoppia bipilis</i> * <i>C. sphaerica</i> <i>Cyta brevirostris</i> <i>Halotydeus insulanus</i> |
| SPRINGTAILS (Collembola): | <i>Achorutes longispinus</i> <i>A. tulbergi</i> <i>A. viaticus</i> <i>Folsomia quadrioculata</i> * <i>F. sexoculata</i> * <i>Isotoma olivacea</i> <i>I. viridis</i> * <i>Lepidocyrtus lanuginosus</i> <i>Onychiurus armatus</i> <i>O. groenlandicus</i> * <i>Sminthurinus niger</i> <i>Xenylla humicola</i> |

| | |
|--|--|
| FLIES (Diptera): | <ul style="list-style-type: none"> *<i>Acroptera frontata</i> <i>Camptocladius curninervis</i> var. <i>polaris</i> <i>C. extremus</i> <i>C. ? lasiops</i> <i>C. longicosta</i> <i>Exechia frigida</i> <i>Limnophora hyperborea</i> <i>L. megastoma</i> *<i>Rhamphomyia caudata</i> <i>Scatophaga varipes</i> <i>Sciara holmgrenii</i> <i>S. pallidiventris</i> <i>S. sp. indet.</i> <i>S. tridentata</i> *<i>Syrphus tarsatus</i> <i>Trichocera lutea</i> Also the adults of many aquatic flies |
| SAWFLY (Hymenoptera): | * <i>Pristophora frigida</i> |
| ICHNEUMONS and BRACONIDS (Parasitic Hymenoptera): | <ul style="list-style-type: none"> <i>Hemiteles septentrionalis</i> <i>Bassus arcticus</i> *<i>Orthocentrus pedestris</i> *<i>Atractodes bicolor arcticus</i> <i>Mesolcius leucopygus</i> *<i>Ichneutes hyperboreus</i> and several others |
| MOTHS (Lepidoptera): | <ul style="list-style-type: none"> *<i>Plutella cruciferarum</i> Another species of moth (not yet collected) |
| BETTER (Coleoptera): | <ul style="list-style-type: none"> *<i>Tachyerges (Orchestes) saliceti</i> *<i>Atheta</i> spp. <i>Phytodecta</i> sp.? |
| APHID (Hemiptera): | * <i>Aphis</i> sp. |
| ENCHYTRAID WORM (Oligochaeta): | <i>Henlea brucei</i> |

Compared with the fauna of more temperate regions, this list is very meagre; compared with the fauna of North-East Land, it has a tropical luxuriance. During two expeditions to the North-East Land region (which here includes the dolerite islands of Hinlopen Strait, and the dolerite areas on the north coast of New Friesland) only *nine species* of animals were found on the dry fjaeldmark and lichen-moss heath. Doubtless more species exist, but not many more. There is one common spider, *Typhochrestus spetsbergensis*, and one other, *Hilaira glacialis*, which we only found at North Cape. Both are small black hunting spiders which probably prey on the two species of land-flies *Camptocladius ? lasiops* and *Sciara* sp., and on the springtail *Achorutes viaticus*. In addition there occurs the scarlet intertidal mite, *Bdella littoralis*, here invading the land. It seems fairly certain that this mite is distasteful to birds, since the latter are seldom seen feeding in the intertidal mud areas in other parts of Spitsbergen, where the mite is very numerous. This fact was especially noted at Klaas Billen Bay, with regard to the Purple Sandpiper. Whether the *Bdella* is eaten by spiders we do not know.

Not only is the fjaeldmark fauna very poor in species, but the number of individuals is extremely small. Careful collecting among the fjaeldmark plants of the islands, or at Cape Eremit, often yielded no animals at all, while only

one or two were to be found on Low Island and North Cape. In fact, it seems quite certain that the insects mentioned above would not by themselves be sufficient to support a spider population, much less a bird population. The real source of food for the spiders is the comparatively large number of aquatic chironomid flies, of which there are three species, all fairly common: *Chironomus lugubris*, *Metriocnemus ursinus*, and *Orthocladius conformis*.

These flies pass their larval and pupal stages in permanent ponds, and fly about over the surrounding tundra, where they are caught by spiders and birds. The two land-birds are the Snow Bunting and the Purple Sandpiper. Here, again, the smaller animals already mentioned are not sufficiently numerous to support by themselves a population of Purple Sandpipers, so that the latter are compelled to feed also upon springtails (*Achorutes viaticus*) which occur in bogs, on pond margins, and on the surface of pools; they also eat the worms (*Lumbricillus aegialites*) found near the drift-line of the sea-shore.

The Snow Bunting subsists on flies, etc., but supplements this diet with the seeds and leaves of plants. It appears, however, to be limited in its distribution in North-East Land mainly by the presence or absence of chironomid flies, since wherever there were flies the buntings were also there, and where there were no flies the buntings were absent. This fact was noticed by Montague on his sledge journey to the north coast.

Finally, there is not a sufficiently dense bunting and sandpiper population to support even the ghost of an Arctic Fox, and the latter where it occurs, must be dependent for its food in summer upon sea-birds, their eggs, and upon carrion.

It is clear that in order to construct a food-cycle for the animals of the North-East Land region, we must include not only the species occurring on the fjaeldmark and lichen-moss heaths, but also those living in fresh-water pools, in bogs, and on the sea-shore. This is really the case in any country, but in the temperate zone the complication of food-cycles in any one plant community is so great that it obscures the fact that the animals in it are closely linked with those of all the other communities around it.

The statements made above about the food-habits of the animals depend mainly on field observations (which are fairly conclusive, e.g. when one sees sandpipers feeding in a place where there is only one species of springtail). These observations agree with what we already know of the food-habits of the animals in other parts of Spitsbergen.

The foregoing account requires qualifying in two ways, in order to give a correct picture of the fauna of this region. In the first place, the animal community described is that found in the barren parts of North-East Land and Hinlopen Strait, where climatic conditions are very severe. There is however good reason for believing that a rather richer fauna would be found at the heads of the fjords which run into the interior of North-East Land.

For instance, Wahlenberg Bay is very barren at its mouth (Cape Idun and the Gylden Islands), but Oxford Peninsula which lies right at the head of the fjord, seems in its vegetation to be much more like Reindeer Peninsula in Liefde Bay (e.g. presence of *Dryas*), and in its birds and mammals. There are Brent Geese (*Branta bernicla hrotah*) and Reindeer there, and our party shot one Bewick's Swan (*Cygnus bewickii*), a rare bird in Spitsbergen. Similar but more favourable conditions probably exist at the inner ends of Lady Franklin Bay and Brandywine Bay, but Murchison Bay appears to be quite barren throughout its length. In just the same way a better fjord climate is

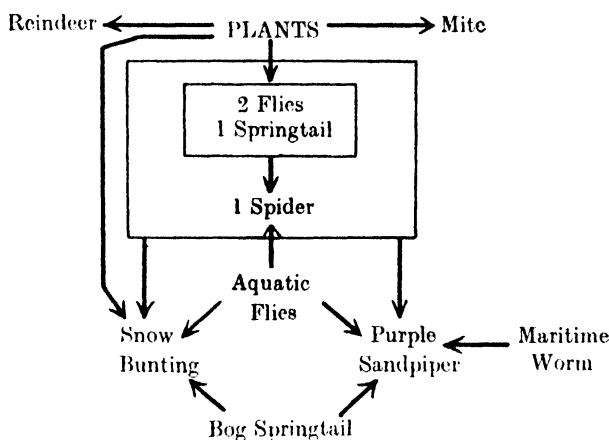


FIG. 2. Food-cycle for the animal community of the barren regions of North-East Land and Hinlopen Strait. Arrows point from species eaten to that which eats it. (The numbers refer to the number of species.)

found at Lomme Bay, on the other side of Hinlopen Strait, the mouth (Cape Fanshawe) being barren, but the inner part possessing *Dryas*, and *Cassiope* heath, together with a corresponding set of animals, e.g. the spider *Erigone psychrophila* and the mite *Rhagidia gelida* occur, and Brent Geese frequent the grass-swamps.

The second point is that the scarcity of land animals in the North-East Land area is to some extent compensated for by the immense abundance of sea-birds, which find a rich food-supply in the sea, and come to land in summer in order to breed. There are two huge colonies of Brünnich's Guillemot (*Uria l. lomvia*) in Hinlopen Strait, one on the Alkrange, and the other on Wahlberg Island. They nest in countless numbers on the dolerite cliff ledges, while above them in still more inaccessible places there are Kittiwakes (*Rissa tridactyla*), which also form independent colonies in other places. The Glaucous Gull (*Larus hyperboreus*) nests near the Guillemots, whose eggs and young form its chief food-supply; while the Kittiwakes are harassed by Skuas. Other sea-birds which form local nesting colonies on cliffs in various parts of this region are the Spitsbergen Puffin (*Fratercula arctica naumanni*), the Little Auk

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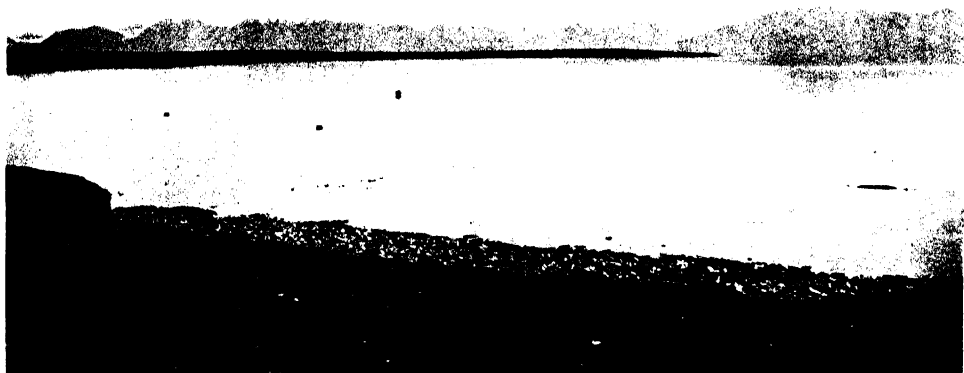
(*Plotus alle*), Mandt's Black Guillemot (*Uria grylle mandtii*) and the Ivory Gull (*Pagophila eburnea*). Fulmar Petrels (*Fulmarus g. glacialis*) are often seen flying about, but do not seem to nest much on the coast, preferring inland cliffs, often nunataks piercing the ice-cap of New Friesland. On low-lying areas there are colonies of Northern Eider Ducks (*Somateria mollissima borealis*) and Arctic Terns (*Sterna macrura*). Two more birds complete the list: the Arctic Skua (*Stercorarius parasiticus*) which divides its attention between eating the eggs of the Eider Ducks and chasing the Kittiwakes in order to rob them of their food; and, finally, the Red-throated Diver (*Colymbus stellatus*) which nests in bogs or on the fjaeldmark, but feeds at sea.

The sea-birds have in many places produced patches of richer vegetation by manuring the ground, and this usually takes the form of a grass-turf. This turf seems to support a slightly more varied fauna of invertebrates than that found on the normal fjaeldmark—a fact noticed in other parts of Spitsbergen also; this point is treated in more detail later on, under Nitrophilous Communities.

IV. LIEFDE BAY.

(a) REINDEER PENINSULA.

Reindeer Peninsula was visited for a short time in 1923, and for about nine weeks in 1924, when it formed the base camp of the expedition. This peninsula, which is about 10 miles long and nearly as broad, consists of gently rolling country, with a range of mountains on the western side, that is, at the base of the peninsula. The ground rises to about 200 ft. (60 m.) above sea-level to a watershed in the centre, from which there are radiating valleys to the coast. The underlying rock is more or less uniform, consisting mainly of red shaly sandstones of Devonian age, mixed with hard quartzites. Above these are various superficial deposits, the most important being boulder-clay, while in the valleys, alluvial deposits occur, derived from the rock or the boulder-clay or from both. There are also a large number of erratic blocks of hard gneiss, some of these being more than 10 ft. (3 m.) high or 20 ft. (6 m.) long. The climate is about the same over the whole of the Peninsula, being slightly more severe on the north side. Frost-action is very prominent in such a damp and open climate, so that a great proportion of the surface, as at Prince Charles Foreland (see 29, p. 242) is occupied by "polygonal soils" of varying types, some of the polygons being "mud-polygons," while others are "stone-polygons." The vegetation occupying these polygonal soils is often different from that on the normal well-drained ground, and this tends to complicate the course of succession and makes it difficult to follow the different stages. The communities on Reindeer Peninsula may best be divided into three series, whose distribution appears to be determined by differences of water-supply during



Phot. A. N. T. Rankin

Phot. 11. Liefde Bay, seen from the south shore of Reindeer Peninsula. The entrance to the bay lies between the point of the Peninsula (in the middle distance) and in front of the mountains. The shore is practically barren of plant or animal life.



Phot. J. Walton

Phot. 12. *Dryas octopetala* growing on boulder clay. The photograph was taken at Klaas Billen Bay in Icefjord, but illustrates the mode of growth of *Dryas* on Reindeer Peninsula, which is an example of the "Dryas Zone."

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the vegetative season. Owing to the fact that the precipitation is almost entirely in the form of snow during the winter (rainfall in summer being comparatively unimportant), the vegetation is dependent on water derived from melting snow. This supply of water fails rather suddenly in many places

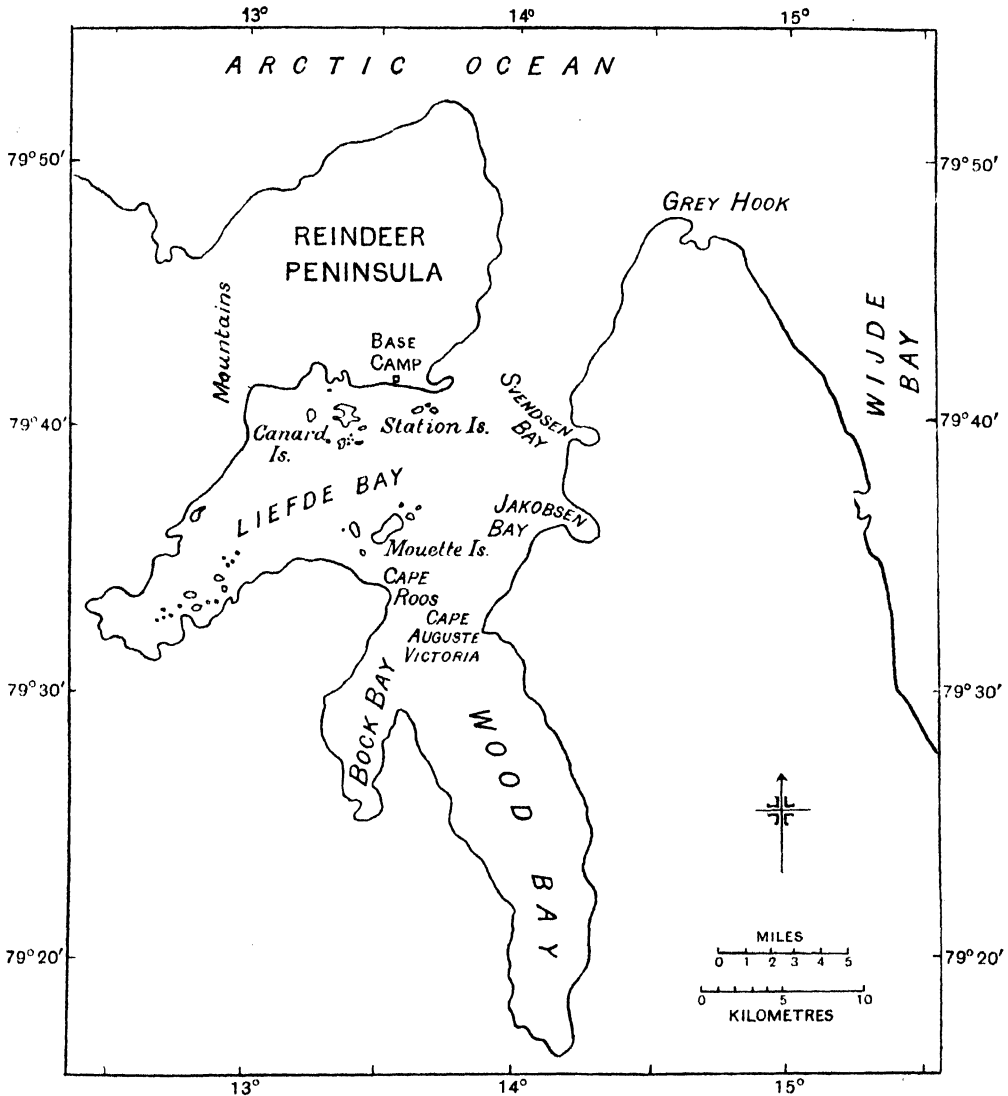


FIG. 3. Sketch-map of the Liefde Bay district (from the chart of Isaakson and the survey of the Swedish Arc of Meridian Expedition, 1899–1902).

towards the end of July (see 8, pp. 166, 167), but the speed with which it does so varies according to the topography. It is obvious therefore, that local differences in the water-content of the soil become more and more pronounced as the summer advances, and can be most easily observed in late summer. A classification of communities based on water-content of the soil in early summer may be quite misleading, since at the beginning of this time

the ground is saturated with snow-water nearly everywhere; places which consist of wet viscous mud in early July may be completely dry and as hard as stone by the beginning of August. We have classified the communities according to the water-supply of the soil, including the time factor, as follows:

- A. Communities on ground dry in autumn to at least 2 ft. (0.6 m.) in depth.
 - (a) Rock outcrops.
 - (b) Fjaeldmark.
 - (c) *Dryas* fjaeldmark.
 - (d) Coastal belt.
 - (e) *Salix polaris* mud-polygon community.
 - (f) Erratic boulders.
- B. Communities on ground damp in autumn either at the surface or not far below it.
 - (a) Stone-polygons.
 - (b) Damp fjaeldmark.
 - (c) Herb slopes.
 - (d) *Ranunculus sulphureus* community.
 - (e) Dried-out tarns.
- C. Bogs, with continuous wet surface.

A. *Communities on ground dry in autumn to at least 2 ft. (0.6 m.) in depth.*

These communities occupy the more steeply sloping or otherwise well-drained places, particularly where there is no boulder-clay.

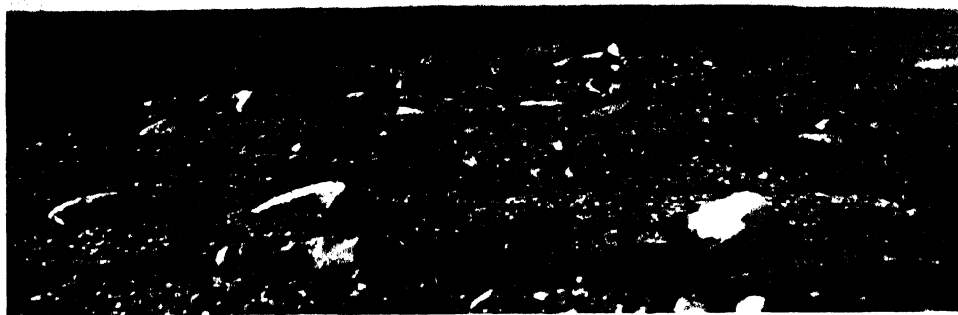
(a) **Rock outcrops.**

The rock outcrops are frequent, but owing to their relative softness they soon weather, the rate of weathering being especially fast in the case of the shale, while even the quartzite is reduced to gravel or stones. As a result of this lithophytes are rather uncommon, and saxicolous lichens are not so prominent as in the gneiss-granite regions. The following lichens were collected on shale *in situ*:

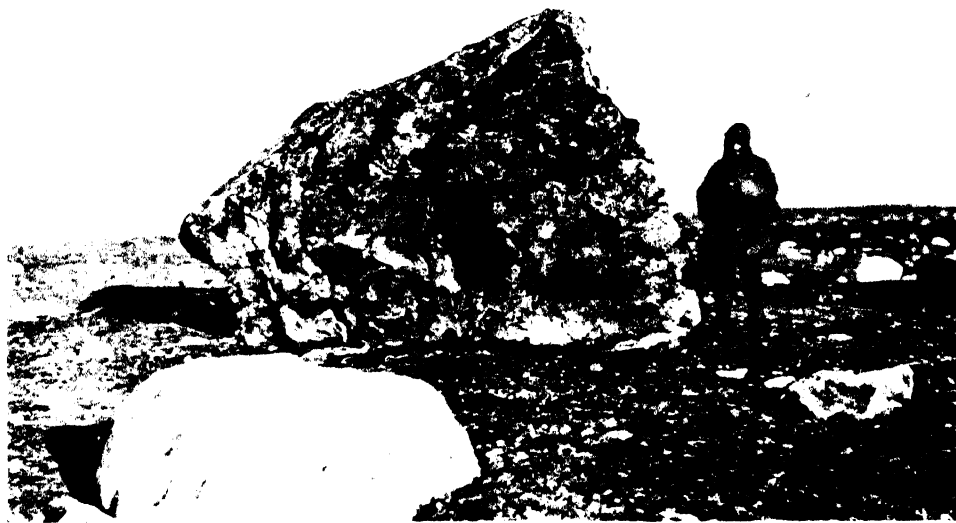
Caloplaca elegans
Lecanora dispersa
Lecidea alpina

Placynthium asperellum
Rhizocarpon geographicum

while *Pertusaria ceuthocarpa* and *Placynthium asperellum* were noticed on quartzite. As the shale weathers away, it forms heaps of gravelly mud, and these are invaded by various plants such as *Stereocaulon alpinum*, *Lecanora tartarea* var. *frigida*, and *Rhizocarpon chioneum*. *Saxifraga oppositifolia* is one of the first of the higher plants to get a footing on the weathering hummocks, together with *Salix polaris*, in the cracks between adjacent stones. Various mosses accompany the phanerogams and lichens; of these the following were observed, viz. *Ditrichum flexicaule*, *Hypnum uncinatum*, *Swartzia montana*,

*Phot. J. D. Brown*

Phot. 13. Reindeer Peninsula, Liefde Bay. Rolling country of which the drier parts are sparsely covered with fjældmark vegetation or *Dryas*. Small erratic blocks of gneiss can be seen scattered about. In the distance are the mountains at the base of the Peninsula.

*Phot. C. S. Elton*

Phot. 14. A large erratic block of gneiss on Reindeer Peninsula. The block supports a vegetation different to that of the rest of the country, which is composed of shales and quartzites.

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and *Tortula ruralis*, all of which are typical constituents of the normal fjaeldmark.

With the continuance of the weathering and colonisation of the hummocks by plants, the vegetation gradually passes over into the next community.

(b) Fjaeldmark (Reindeer pasture).

This community covers large tracts of rolling country, occurring on weathered rock or on alluvial deposits, and a good idea of its appearance can be obtained from the accompanying photograph (Pl. XXX, Phot. 13). It is the chief grazing ground of Reindeer in the early part of the summer. The soil is generally shallow (about 1 to 2 ft. = 0.3 to 0.6 m.) and quite dry in autumn; small stone-polygons occur in slightly damper areas, but the stones are small and the vegetation is not affected by them. As might be expected, the floristic composition varies from place to place, but generally no one plant is dominant, although *Salix polaris* and *Saxifraga oppositifolia* are perhaps the commonest species. Mosses and lichens are abundant and in places may be co-dominant with the phanerogams. Nowhere, however, do the lower plants dominate over the higher ones, while *Racomitrium lanuginosum*, which forms such characteristic communities at Aldert Dirkses Bay and on the dolerite areas, is almost completely absent.

The following is a list of the most important species occurring in this community, but it is by no means complete, especially as regards the lower plants:

| PHANEROGAMS, etc. | | | |
|--|-------|--|---------|
| <i>Alsine rubella</i> | r. | <i>Polygonum viviparum</i> | r. |
| <i>Cerastium alpinum</i> | o.—f. | <i>Potentilla emarginata</i> | r. |
| <i>C. regelii</i> | o. | <i>Ranunculus sulphureus</i> | r. |
| <i>Cochlearia</i> | o. | <i>Salix polaris</i> | o.—c.d. |
| <i>Draba alpina</i> | r. | <i>Saxifraga caespitosa</i> | o.—f. |
| <i>D. lactea</i> | o. | <i>S. cernua</i> | o.—f. |
| <i>D. oblongata</i> | o. | <i>S. flagellaris</i> | l.f. |
| <i>Equisetum arvense</i> var. <i>arcticum</i> | r. | <i>S. nivalis</i> | r.—o. |
| <i>Luzula confusa</i> | f.—a. | <i>S. oppositifolia</i> | o.—l.d. |
| <i>Oxyria digyna</i> | o.—f. | <i>Silene acaulis</i> | r. |
| <i>Papaver radicatum</i> | o.—f. | <i>Stellaria longipes</i> | r. |
| <i>Pedicularis hirsuta</i> | o.—f. | <i>Taraxacum nivale</i> | r.r. |
| BRYOPHYTES. | | | |
| <i>Blepharostoma trichophyllum</i> | | <i>Orthothecium chryseum</i> | |
| <i>Brachythecium salebrosum</i> var. <i>arcticum</i> | | <i>Polytrichum alpinum</i> | o.—a. |
| <i>Bryum</i> sp. (sterile) | | <i>Sphenobolus</i> sp. | |
| <i>Cynodontium virens</i> | l.a. | <i>Swartzia montana</i> | |
| <i>Ditrichum flexicaule</i> | f. | <i>Timmia austriaca</i> var. <i>arctica</i> | |
| <i>Hypnum uncinatum</i> | o. | <i>Tortula ruralis</i> | |
| <i>H. revolutum</i> | f.—a. | <i>Webera cruda</i> | |
| LICHENS. | | | |
| <i>Alectoria ochroleuca</i> | | <i>Cladonia</i> sp. | o.—f. |
| <i>Caloplaca cerina</i> | | <i>Dufouria muricata</i> | |
| <i>C. cinnamomea</i> | | <i>Lecanora tartarea</i> var. <i>frigida</i> | a. |
| <i>Candelariella vitellina</i> | | <i>Peltigera canina</i> | |
| <i>Cerania vermicularis</i> | l.f. | <i>Pertusaria oculata</i> | |
| <i>Cetraria islandica</i> | f.—a. | <i>Rinodina turfacea</i> | a. |
| <i>C. nivalis</i> | o.—a. | <i>Sphaerophorus globosus</i> | |

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The resemblance between this and the fjaeldmark at Prince Charles Foreland, omitting the *Dryas* from the latter, is striking (29, p. 244). The relative frequency of lower plants in the fjaeldmark is shared by all areas in Spitsbergen with a marked coastal climate and also by Bear Island.

The fauna of the ordinary fjaeldmark.

Undoubtedly the Reindeer (*Rangifer spitsbergensis*), although greatly reduced in numbers now, exert an important effect on the vegetation. They were observed in the early summer grazing on various plants, such as flowering *Saxifraga oppositifolia* and *Salix polaris*, but exhibited a special preference for *Oxyria digyna*. For instance, Clutterbuck watched a stag which went out of its way to go from clump to clump of *Oxyria*, while on several occasions, tracks of Reindeer were followed, and for some distance every plant of *Oxyria* was found to have its leaves, and sometimes its flowers, nibbled. About August the Reindeer mostly desert the fjaeldmark for the summer grasses (*Arctophila fulva*, etc.) which have then grown up in the swamps around tarns; but they still continue to eat the *Oxyria* on the dry regions. It is at this time that the Reindeer store up under their skins the thick layer of fat which they require as a reserve for the winter, and which is produced in a surprisingly short time. In winter, they probably migrate to hilly country elsewhere, where they frequent the moss-lichen heaths (see Wijde Bay, p. 232).

The following is a list of the animals living on the general fjaeldmark or Reindeer pasture:

| | |
|---------------------------|---|
| BIRD: | Purple Sandpiper (<i>Erolia m. maritima</i>) |
| MAMMALS: | Arctic Fox (<i>Canis lagopus</i>) Reindeer (<i>Rangifer spitsbergensis</i>) |
| SPIDERS (Araneida): | Typhochrestus spetsbergensis Erigone psychrophila |
| MITES (Acarina): | Bdella decipiens Halotydeus insulanus Rhagidia gelida Sphaerozetes notatus |
| SPRINGTAILS (Collembola): | Achorutes longispinus A. tullbergi var. concolor A. viaticus Folsomia fimetaria F. quadrioculata Onychiurus armatus var. arcticus O. groenlandicus |
| FLIES (Diptera): | Camptocladius extremus C. longicosta Diamesa arctica (? aquatic) Limnophora hyperborea Phronia egregia Scatophaga ? varipes (dung fly) Sciara holmgrenii S. pallidiventrif S. praecox S. sp. |
| WORM (Oligochaeta): | Henlea brucei |

In addition to the Purple Sandpiper, the Turnstone (*Arenaria i. interpres*) and the Sanderling (*Crocethia alba*) occur in small numbers; but since both these waders feed on the shore or in estuaries, and do not appear to eat the dry fjældmark animals, they do not play any part in the food-cycle of the land community, although they nest there. It will be noticed that the Snow Bunting (*Plectrophenax nivalis*) and the Ptarmigan (*Lagopus mutus hyperboreus*) do not appear in the list. The former only comes on the mountains, for the reason given on p. 228.

Besides the flies given in this list, there are large numbers of chironomid flies, which breed in tarns and streams, and in bogs, and which fly about on the dry parts of the peninsula when they become adult. These flies form an

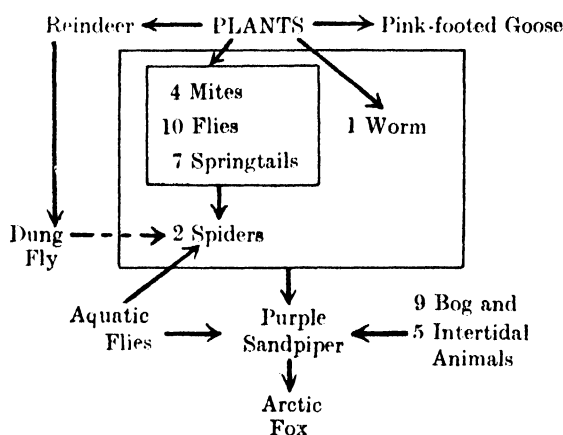


FIG. 4. Food-cycle for the animal community of the fjældmark (Reindeer pasture) on Reindeer Peninsula. The arrows point from the animal eaten to that which eats it. This diagram should be compared with the food-cycle for North-East Land (Fig. 2, p. 211). (The numbers refer to the number of species.)

important article of diet for Spiders, and probably to some extent also for the Sandpipers. They are most numerous in July. The following is a list of the species of chironomid flies which were caught:

Camptocladius globifer, *C. ? lasiophthalmus*, *C. pumilio*, *Chironomus lugubris*, *Cricotopus basalis*, *C. humeralis*, *Metriocnemus cataractorum*, *M. obscuripes*, *M. ursinus*, *Orthocladius consobrinus*, *O. petraeus*, *Psectrocladius borealis*, *P. limbatellus*.

It will be noticed that two species of *Camptocladius* have been listed as dry-land forms, and three as aquatic; this is based only on the circumstantial evidence obtained in various parts of Spitsbergen, and there is no actual record of their breeding places. The same applies to *Diamesa arctica*, which may really be aquatic.

Apart from chironomid flies, the actual number of individuals of invertebrates in this community is very small indeed. One can hunt for hours through plants, shaking them out carefully in order to get springtails, mites, etc.,

without finding more than a dozen specimens. Spiders are the most obviously numerous inhabitants of the fjaeldmark, since they have an abundant food-supply in the form of chironomid flies. Comparing the fauna of Reindeer Peninsula with that of North-East Land, it will be seen that there are about four times as many species of land-animals in the fjaeldmark of the former as in that of the latter, but that the main features of the food-cycle are much the same. Among the new arrivals are the worm (*Henlea brucei*), the Pink-footed Goose, and the Arctic Fox. The latter is however extremely scarce, only two foxes having been seen by us in two summers, and it seems probable that there is not enough in the way of food on land to support it on the Peninsula, and that it only spends a small fraction of its working days actually on it. The foxes probably go up into the mountains, where there are ptarmigan, or else frequent the neighbourhood of sea-bird colonies. In other words, there are not enough invertebrates to support a bird population large enough to maintain even one or two foxes, on an area of something like 80 to 100 square miles. This gives one some idea of the sparseness of the population of lower animals and birds on Reindeer Peninsula. At the same time, it may be noted that nearly half of the fjaeldmark and heath species of Spitsbergen (as listed on pp. 208-209) are represented on this area. It is the number of individuals which is so low. This fact is again reflected in the enormous size of the territories of the Purple Sandpipers, whose nests may be several miles apart.

(c) *Dryas* fjaeldmark.

This occurs wherever the surface is free from boulder-clay or other extrinsic mud, and where the drainage is good—e.g. hill-tops and slopes. The soil is gravel mixed with a little mud, and it is extremely hard and dry two or three weeks after the end of the melting of the snow. *Dryas octopetala* (Pl. XXIX, Phot. 12) is the dominant plant, usually occurring as an almost pure community, but *Carex misandra* may also be present. Lichens are present, especially *Cerania vermicularis* and *Cetraria nivalis*, but mosses are rare. Where the ground was very exposed, the *Dryas* plants could be seen growing away from the north, or north-east, the direction of the prevailing summer winds (see 26, p. 214). Elsewhere the plants exhibited no common direction of growth.

As the *Dryas* community appears to be restricted to well-drained soil, it seems likely that much of the fjaeldmark, which occurs on alluvial muds, will never pass into *Dryas* fjaeldmark, and in this case the mixed fjaeldmark may be looked on as an edaphic climax. This relationship between *Dryas* and mixed fjaeldmark is very similar to that noted at Cape Boheman where the rocks are of a similar nature (see 29, pp. 250-1).

Animal life is very scarce in the *Dryas* fjaeldmark (possibly owing to the dryness of the plants and the soil) with the exception of a species of small fly, *Sciara pallidiventris*, which was several times found abundantly on the leaves

before the flowers had opened, and which probably breeds in the plants and which occurs also on the general fjaeldmark. Chironomid flies which have bred in fresh-water, also occur as strays; but on this peninsula, the *Dryas* usually grows on the hill-tops away from the tarns, so that these flies are not so common as, for instance, at Klaas Billen Bay, where they swarm on the flowers of *Dryas* at the end of July. Spiders occur among the *Dryas*, presumably preying on the flies. The only other constant inhabitant of the *Dryas* areas is the Turnstone, which shows a marked, though not exclusive preference for nesting in these places. This bird feeds on the sea-shore, and really plays no part in the food-cycle of the dry parts of the Peninsula. It will be seen that the appearance of a higher form of vegetation (*Dryas*) as a result of an improvement in climate, is not necessarily accompanied by an increased richness in the animal life, although the latter does show such an increased richness on the normal fjaeldmark and in other associations.

(d) Coastal belt.

A narrow zone around the coast supports rather different vegetation from that found inland. This must be due to the salt spray blown over the land (which is usually less than 10 ft. (3 m.) above sea-level), since a salt efflorescence appears on the surface when this soil dries. The zone is of varying width, with a maximum of 50 yds. (45 m.). An interesting feature, which no doubt is of importance in connection with the vegetation, is that the first snows of autumn melt on this belt, while remaining farther inland. A certain number of plants are characteristic of this zone, being rare or absent elsewhere, e.g. *Cochlearia groenlandica*, *Glyceria angustata* (limited to boulder-clay), *Potentilla emarginata*, and *Stellaria humifusa*. *Silene acaulis* is common locally in the coastal belt, and its flowers are visited during sunny weather by two flies, *Scatophaga varipes* and *Limnophora hyperborea*. Other plants found generally on the fjaeldmark also occur, the vegetation being generally modified fjaeldmark which may be considered as having been derived from the normal type as a result of the salinity of the soil and air. A corresponding coastal belt is found on similar rocks at Cape Boheman (in Icefjord), and is probably of general occurrence in the country, where circumstances permit.

(e) *Salix polaris* mud-polygon community.

The boulder-clay, which occurs in large amounts on certain parts of the peninsula, is generally deeper and tends to hold the water more firmly in the lower layers than the shale and sandstone debris. As a result, mud-polygons are formed by winter frost expansion, and a peculiar community is produced. These mud-polygons consist of areas of various shapes, often hexagonal, which are higher in the middle and surrounded by a sort of channel (the general appearance is shown in Pl. XXIX, Phot. 12, which however shows *Dryas*). The polygons may again be divided into smaller ones, caused by drying. The

soil is much drier in autumn than in the communities described later, but has certain characters in common with them. The centres of the polygons are usually almost bare, or are occupied by scattered lichens and plants of *Saxifraga oppositifolia*. The channels, however, are filled with prostrate mats of *Salix polaris*, which is here usually dominant. Other species of the usual fjældmark flora are associated with the dwarf willow. This type of community is well illustrated in the account of Klaas Billen Bay in our previous paper (29, Pl. III, fig. 1, p. 262).

(f) Erratic boulders.

There are a number of erratic boulders of gneiss scattered over the whole area, some of them being of great size (Pl. XXX, Phot. 14). The communities on these rocks differ from those on the sandstone and shale, partly because of the chemical and physical differences, and partly because the hardness of rock allows lithophilous plants to become established before the surface has weathered away. On the rock surfaces themselves there is a rich flora of crustaceous and foliose lichens, the following having been recorded:

Alectoria nigricans
Candelariella vitellina
Gyrophora erosa
G. hyperborea
Lecanora tartarea var. *frigida*
Lecidea pantherina
Parmelia alpicola

Parmelia pubescens
Physcia tribacia
Placynthium asperellum
Rhizocarpon chioneum
R. grande
Rinodina turfacea

There are very few animals living among these lichens, but the small spider *Erigone psychrophila* was often found running over the boulders probably in search of small flies (e.g. *Sciara* ? *holmgrenii*) which fly about and settle there.

In hollows and slight crevices where a little organic debris can collect, mosses are associated with the lichens, the following species being found:

Bartramia ithyphylla
Camptothecium nitens
Cynodontium virens
Ditrichum flexicaule var. *densum*

Grimmia apocarpa
Hypnum uncinatum
H. vaucheri
Tortula ruralis

Lecanora tartarea var. *frigida* occurs encrusting the mosses.

On the plateau it was noticed that some of the gneiss blocks had a black cap of lichens, the lower part of the block below a more or less definite line being devoid of them. The average height of the bottom of the cap from the ground was about 17–18 in. (0.5 m.). In this district the cap is usually composed of *Parmelia pubescens* and *Gyrophora* spp.

One large flat boulder about 3 ft. (1 m.) in height had a hollow 4 ft. (1.2 m.) in diameter, and 4 in. (0.1 m.) deep. This was colonised by plants, there being quite a definite series of zones:

(1) On the rock outside: various crustaceous lichens.

(2) In crevices and hollows: *Andreaea papillosa*, *Cynodontium wahlenbergii*, *Grimmia apocarpa*, with *Lecanora tartarea* var. *frigida* on the mosses.

(3) A moss zone: *Racomitrium lanuginosum*, *Hypnum uncinatum*, *Polytrichum alpinum*, together with encrusting *Lecanora tartarea* var. *frigida*.

(4) Moss mat with *Lecanora tartarea* in places. *Hypnum uncinatum* dominant with a few lichens. No *Racomitrium* here.

(5) Mosses with phanerogams mixed. *Hylocomium splendens*, and other mosses a. and d.

| | | | |
|--------------------------|----|------------------------------|----|
| <i>Alsine rubella</i> | r. | <i>Potentilla emarginata</i> | a. |
| <i>Cerastium alpinum</i> | f. | <i>Saxifraga cernua</i> | o. |
| <i>Luzula confusa</i> | d. | Grass | o. |

(6) Finally, in the centre was a closed mat of *Luzula confusa* and various mosses.

This series of zones thus represents the course of succession on gneiss in this region, the development having occurred directly on bare rock without any external interference, except a little manuring by Reindeer and Snow Buntings. The existence of these transported blocks of gneiss on a coastal area otherwise lacking that rock, forms a sort of natural experiment which enables us to compare succession on two rocks in the same climate. The later stages (Zones 3 to 6) supported a miniature animal community of their own, consisting of two mites (*Halotydeus insulanus* and *Sphaerozetes notatus*), a small fly (*Sciara ? holmgrenii*), and a springtail (*Onychiurus* sp.) preyed on by the spider *Erigone psychrophila*. These were all more abundant than on the ordinary fjaeldmark. As already mentioned, dung of Snow Buntings showed that this bird, although seldom found on Reindeer Peninsula, had visited this boulder on migration; while the abundant dung of Reindeer proved that they had been attracted by the plants.

B. *Communities on ground damp in autumn either at the surface or not far below it.*

The communities included in this category are a rather mixed collection which do not always seem to have any definite relation to one another. However it is possible to arrange many of them in a series which illustrates the succession which has taken place. In the account which follows, an attempt has been made to reconstruct the probable course of succession depending on the changes brought about in the surface through frost-action. These changes have been considered by one of us elsewhere (8) and to that paper the reader must be referred. Naturally the first stage will be the rock outcrops which have already been described above. As the rocks weather on this type of terrain, areas covered with rock debris would be produced, but apparently most of the area has progressed to a further stage than this since no "block-plains" of any great size were seen.

(a) **Stone-polygons.**

With the continued frost-action, the stones are gradually pushed out centrifugally from certain centres, the ground between consisting of wet mud, sometimes with a few small stones. These stone networks or circles are termed "stone-polygons," and they cover large tracts of Reindeer Peninsula, where they often occupy a zone round the edges of the ponds and lakes. The polygons are of varying sizes up to 16 ft. (c. 5 m.) or more, while the stone borders may be 1 ft. (0.3 m.) or more wide. For the theories as to the probable mode in which they are formed the reader is referred to the paper mentioned above (8).

It is possible to divide the vegetation of the polygons into three distinct zones, viz. (1) centres, (2) edge of centres and of borders, (3) tops of borders. The following list, which is compiled from two sets of polygons, gives an idea of the vegetation. *Saxifraga oppositifolia* (Pl. XXXV, Phot. 22) is the most characteristic plant of the polygon centres, while *Cerastium regelii* is also usually present; but the vegetation is always scattered. Encrusting lichens are generally found, and are normally the first invaders of the mud.

On the edges of the centres the vegetation is much richer, and usually forms a closed mat, mosses being prominent. The tops of the borders are occupied by the species of dry places only.

| | 1 | 2 | 3 |
|-------------------------------|----|----|----|
| PHANEROGAMS: | | | |
| <i>Alsine rubella</i> | — | × | — |
| <i>Cerastium alpinum</i> | o. | o. | o. |
| <i>C. regelii</i> | f. | f. | — |
| <i>Cochlearia officinalis</i> | — | × | — |
| <i>Draba alpina</i> | r. | r. | — |
| <i>Juncus biglumis</i> | — | r. | — |
| <i>Oxyria digyna</i> | — | f. | — |
| <i>Papaver radicatum</i> | — | r. | f. |
| <i>Saxifraga caespitosa</i> | o. | o. | — |
| <i>S. cernua</i> | — | f. | — |
| <i>S. nivalis</i> | — | o. | — |
| <i>S. oppositifolia</i> | a. | f. | o. |
| Grass | r. | o. | — |
| MOSSES: | | | |
| <i>Bryum pendulum</i> | × | — | — |
| <i>B. sp.</i> | — | × | — |
| <i>Ditrichum flexicaule</i> | — | × | — |
| <i>Encalypta commutata</i> | — | × | — |
| <i>Hypnum turgescens</i> | × | × | — |
| <i>Orthothecium chryseum</i> | — | × | — |
| <i>Timmia austriaca</i> | — | × | — |
| LICHENS: | | | |
| <i>Cetraria islandica</i> | — | o. | — |
| <i>Lecanora tartarea</i> | f. | o. | — |
| var. <i>frigida</i> | a. | — | — |
| <i>Rinodina turfacea</i> | — | o. | — |
| <i>Stereocaulon alpinum</i> | — | o. | f. |

The resemblances between this table and the lists given for Prince Charles Foreland (29, p. 243) are significant, while the restriction of many of the species to the edges of the centres of the polygons is a striking phenomenon.

(b) Damp fjaeldmark.

After the polygons have become completely mapped out, the drainage in the channels tends to reduce the rate of comminution of the stones, but this proceeds gradually until sometimes the polygons completely disappear, leaving an area composed entirely of mud or fine soil, which at first is arranged in mud-polygons, but may later lose all trace of polygon formation. During this process the drying centres are gradually invaded by plants until an open community or type of fjaeldmark is produced. As in the polygon channels the chief species are *Saxifraga oppositifolia* and *Cerastium regelii*. Other phanerogams also occur, the floral constitution varying somewhat from place to place. Most of the species in the above table are found.

(c) Herb slopes.

If such an area becomes somewhat drier (e.g. on slopes, where the drainage is better) a more closed community may develop, the ground being invaded by many species. These herb slopes merge above into the ordinary dry fjaeldmark, while below they pass gradually into marsh dominated by *Juncus biglumis* and *Alopecurus alpinus*. In one region the plants occurring were as follows, this list giving a good idea of the type of community:

| | | | |
|----------------------------------|----|-----------------------------|-------|
| <i>Cardamine bellidifolia</i> | r. | <i>Oxyria digyna</i> | f. |
| <i>Catabrosa algida</i> (vivip.) | f. | <i>Papaver radicatum</i> | f. |
| <i>Cerastium regelii</i> | f. | <i>Salix polaris</i> | o. |
| <i>C. alpinum</i> | f. | <i>Saxifraga caespitosa</i> | f. |
| <i>Draba alpina</i> | o. | <i>S. cernua</i> | f. |
| <i>D. lactea</i> | o. | <i>S. nivalis</i> | o.—f. |
| <i>Juncus biglumis</i> | f. | <i>S. oppositifolia</i> | l.d. |
| <i>Luzula</i> sp. | f. | <i>Stellaria longipes</i> | o. |
| Mosses | f. | | |

(d) *Ranunculus sulphureus* community.

This is developed on soil of about the same dampness as the last two and also on slightly damper ground. It has probably in some cases been developed from stone-polygons, but seems often not to have passed through that stage. The community is characteristically found in the hollows by the ridges of sandstone outcrops. The most striking, though not necessarily the dominant, plant is *Ranunculus sulphureus*, while *R. nivalis* replaces this species locally. Other species which usually occur are given below, but many additional species may be present in single localities:

| | | | |
|--------------------------------|-------|-----------------------------|-------|
| <i>Alsine rubella</i> | o.—f. | <i>Luzula confusa</i> | r.—f. |
| <i>Cerastium regelii</i> | o. | <i>Oxyria digyna</i> | f. |
| <i>Cochlearia groenlandica</i> | r.—f. | <i>Saxifraga caespitosa</i> | o.—f. |
| <i>Draba alpina</i> | r.—o. | <i>S. cernua</i> | o. |
| <i>Juncus biglumis</i> | f. | Mosses | f.—a. |

This community is obviously intermediate between the last and the *Juncus* bog, and this idea is borne out by observations made on a long transect running from the coast some way inland.

(e) **Dried-out tarns.**

There are a number of tarns scattered about which appear to have been permanent at one time, but are now dried up by the middle or end of the summer. This drying up may perhaps be periodic over a long term of years, and is possibly controlled by the Brückner Cycle of 35 years in snow and rainfall. In any case, during the dry period they tend to be invaded by plants from the drier communities around, while at the same time frost-action has increased and differentiation of the old tarn-beds into stone-polygons is in active process. The onset of drying up must have been comparatively recent, since there are practically no surface rock-lichens except on the higher parts of the stones, where they would have projected from the water. Since different tarns have naturally reached slightly different stages in the succession to drier-type conditions and since, also, the edaphic and other conditions in the different tarns vary, they cannot be included in any definite manner in the scheme already sketched.

Generally speaking, stone-polygon formation is as yet only in the early stages, a complete network not yet having been formed, while in some places the rock outcrops in the former bed have not yet weathered sufficiently for the commencement of stone-polygon formation. Some of the polygons had gravel centres, indicating imperfect differentiation of the mud and stones, while there were stony channels between adjacent rings or borders of polygons, which were thus not yet united. The most striking feature, which is shown in most of the cases examined, is the presence of dead or dying *Hypnum turgescens* and other normally submerged species of mosses, these remains being often covered partially with encrusting lichens, chiefly *Collema*. The flora of the stone-polygons seems to be similar to that of others occurring in their normal position, there being almost bare mud centres with scattered *Saxifraga oppositifolia*, *Lecanora tartarea*, *L. upsaliensis*, and *Rinodina turfacea*, a thick growth of various plants on the mud margins, and lichens only on the stone borders. The presence of *Ranunculus sulphureus* and *Juncus biglumis* suggests that these polygons, as might be expected, are rather damper than the normal ones. In one case the following mosses were found on the mud margins of the polygons:

| | |
|--|---------------------------|
| <i>Brachythecium salebrosum</i> var. <i>arcticum</i> | <i>Hypnum stellatum</i> |
| <i>Bryum obtusifolium</i> | <i>H. turgescens</i> |
| <i>B. pallens</i> | <i>Philonotus fontana</i> |
| <i>B. pendulum</i> | <i>Swartzia montana</i> |
| <i>Camptothecium nitens</i> | <i>Tortula ruralis</i> |

Many of these are typical bog species, although not occupying the lowest zones.

With the possible exception of one or two species of flies of the genus *Camptocladius* (which may turn out to breed only in these places), the fauna of the various damp communities presents no special features of interest,

since it is merely transitional between that of the dry fjældmark on the one hand and that of the bogs on the other. The mixed nature of these animal communities is well illustrated by the fauna of one of the dried-out tarns, in which spiders (*Erigone psychrophila*) were living on the dry outcrops among stones, depending for their food on chironomid flies from the nearest tarn; while amongst the drying *Hypnum turgescens* and wet gravel of the hollows, was a typical bog community consisting of two oligochaete worms (*Henlea brucei* and *Mesenchytracus eltoni*) and two springtails (*Anurida granaria* and *Folsomia quadrioculata*). At the junction of these two habitats, amongst lichen-encrusted *Hypnum*, the spiders were abundant and probably preying both on the chironomid flies and on the *Folsomia*. The Purple Sandpiper commonly feeds in the damp areas.

C. Bogs.

Bogs, usually dominated by mosses, occur around many of the tarns and along the streams. Where the latter are on a slope, the moss-bog is narrow; but in shallow, gently sloping valleys the overflow of the snow-water produces a wide bog extending some way on either side of the stream, and sometimes filling up the whole valley bottom. The data collected were not sufficient to enable us to make any accurate distinctions between different types of bog communities. The water in this region always has a neutral or somewhat alkaline reaction so that acid peat bogs are not found. Consequently the only differences in the moss flora seem to be related to the amount of submergence and the height of the water table at different times in the summer. The moss flora varies very considerably from one bog to another, but the following are found submerged either in tarns or streams:

Hypnum brevifolium
H. fluitans (group Rotac)
H. giganteum

Hypnum scorpioides
H. stellatum

Away from the water there are many mosses, the species being the usual bog ones (see Cape Boheman, 29, p. 254).

Around one tarn on the plateau at about 150 ft. (47 m.) the following zones were recognised:

1. In the water: mud bottom with patches of *Hypnum scorpioides* and *H. fluitans*, the open parts covered with a felt of algae, amongst which were various Entomostraca, including ostracods and *Lepidurus arcticus*, with *Daphnia pulex* swimming in the water itself.

2. Grass-swamp: the inner region of this was encroaching on the *Hypnum* which was growing thickly among the grass. Large numbers of chironomid flies were resting on the stems and settling on the water surface, viz. *Chironomus lugubris*, *Orthocladus petraeus*, *Cricotopus basalis* and *Metriocnemus ursinus*, together with the land-fly *Sciara ? holmgrenii*.

3. Farther out, other mosses, e.g. *Webera nutans*, *Polytrichum strictum*,

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appeared with the *Hypna*, the grass being still abundant. There were also occasional plants of *Cardamine pratensis* and *Ranunculus hyperboreus*, together with small brown fungi, *Dictyolus retirugus*. Reindeer dung was very common here and was surrounded by *Hypnum brevifolium*, and covered with the small orange fungus *Cheilymenia coprinaria*, while in the dung there were enormous numbers of the springtail *Achorutes longispinus* and the worm *Henlea brucei*—inhabitants also of the moss itself.

4. Moss-bog with little grass. *Ranunculus hyperboreus* frequent in places, with scattered *Cardamine*.

5. Area of small stone-polygons, with very narrow shale borders. The following plants were noticed here:

| | |
|--------------------------------|--------------------------------|
| <i>Cardamine pratensis</i> | <i>Saxifraga oppositifolia</i> |
| <i>Cerastium regelii</i> | <i>Nostoc</i> sp. |
| <i>Cochlearia groenlandica</i> | Black encrusting lichens |
| <i>Ranunculus hyperboreus</i> | |

6. Normal fjaeldmark.

This illustrates the normal sequence of communities round tarns. A large stream-bog lying in a wide flat valley and receiving late snow-water from the surrounding hills was examined. There was an almost solid turf of mosses, with many phanerogams; the mosses *Ditrichum flexicaule*, *Hypnum brevifolium*, *H. vernicosum*, and *Orthothecium chryseum*, were collected, but there were doubtless many others. The following phanerogams were observed and the list gives some idea of the floristic composition of these bogs:

| | | | |
|--------------------------------|------|---------------------------------|----|
| * <i>Alopecurus alpinus</i> | c.d. | <i>Luzula confusa</i> | r. |
| * <i>Arctophila fulva</i> | f. | <i>Oxyria digyna</i> | o. |
| <i>Cardamine bellidifolia</i> | r. | <i>Papaver radiculatum</i> | r. |
| <i>C. pratensis</i> | o. | * <i>Ranunculus hyperboreus</i> | f. |
| <i>Cerastium alpinum</i> | o. | <i>R. sulphureus</i> | f. |
| <i>C. regelii</i> | o. | <i>Saxifraga caespitosa</i> | o. |
| <i>Cochlearia groenlandica</i> | f. | <i>S. cernua</i> | f. |
| <i>Draba lactea</i> | o. | <i>S. flagellaris</i> | r. |
| <i>D. oblongata</i> | o. | <i>S. nivalis</i> | f. |
| * <i>Juncus biglumis</i> | f. | <i>Stellaria longipes</i> | f. |

On the whole, the species marked with an asterisk are the most characteristic plants of bogs on Reindeer Peninsula and other areas in Liefde Bay on Devonian sandstones. On the more interior parts, such as the Mouette Islands, *Eriophorum scheuchzeri* is found, while the moss *Mnium hymenophyllum* also occurs.

A number of springtails and worms, together with a few mites, are found in the moss-bogs on Reindeer Peninsula, these being as follows:

| | |
|---------------------------|---|
| SPRINGTAILS (Collembola): | <i>Achorutes longispinus</i> |
| | <i>A. tulbergi</i> var. <i>concolor</i> |
| | <i>A. viaticus</i> |
| | <i>Agrenia bidenticulata</i> |
| | <i>Anurida granaria</i> |
| | <i>Folsomia quadrioculata</i> |
| | <i>Onychiurus groenlandicus</i> |
| WORMS (Oligochaeta): | <i>Henlea brucei</i> |
| | <i>Mesenchytraeus eltoni</i> |
| MITE (Acarina); | <i>Penthaleus</i> sp. |

Spiders (*Erigone psychrophila*) may often be found running about on the surface of mosses, where they probably catch the many chironomid flies coming from the water, and springtails from the moss. It is probable that the larvae of certain species of chironomid flies will be found living in moss-bogs: for instance, *Metriocnemus cataractorum* was only found by stream-bogs, while *Camptocladius pumilio* is also possibly a bog species.

Purple Sandpipers feed on worms and springtails in these areas, and also on chironomid flies. Another bird of moss-bogs is the Red-throated Diver (*Colymbus stellatus*), which makes its nest of mosses on the edge of a tarn, but feeds at sea.

At least three species of springtails occur in open bare places by the margin of streams and on the surface of pools; these are *Achorutes viaticus*, *Agrenia bidenticulata*, and *Xenylla humicola*. Of all the species of animals mentioned above, only two are actually confined to moss-bogs, namely *Anurida granaria* and *Mesenchytraeus eltoni*, the others also occurring on dry fjaeldmark. The bogs differ from the drier areas in the almost complete absence of mites and of most of the flies found in the latter regions, and in the enormously greater density of the worm and springtail population.

(b) MOUNTAIN SLOPES INSIDE LIEFDE BAY.

The districts included in this account are the mountains at the foot of Reindeer Peninsula, Cape Roos district (between Bock Bay and Liefde Bay) and part of Wood Bay. The country in these districts, instead of being flat like Reindeer Peninsula, is much more mountainous, the land rising fairly quickly from the sea to as much as 4400 ft. (1320 m.) in places (Pl. XXIX, Phot. 11, Pl. XXX, Phot. 13). Although the lowest slopes are more or less stabilised, the upper ones are mostly of the nature of scree, the material varying from large blocks to fine muddy shale. As a result of the generally good drainage, polygonal soils are of little extent in the region and are often quite absent. Owing to the short visits made to these localities, it was impossible to obtain data of all the communities. We shall therefore restrict our remarks to the dry types.

The vegetation may be divided into two main sections:

- (1) Fjaeldmark.
- (2) *Dryas* community.

(1) Fjaeldmark.

Most of the country is occupied by this type of vegetation, the master factor being the instability of the soil which prevents effective colonisation and maintains an open community. In these districts, owing to more favourable climatic conditions, *Dryas octopetala* is an important constituent of the fjaeldmark, but many other species are also present. As in most unstable places, *Saxifraga oppositifolia* is a prominent plant, together with *Salix polaris* and *Cerastium alpinum*. It is difficult to give any list which will

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represent the flora adequately, since it varies from place to place according to the instability and nature of the substratum. As a rule more and more plants come in as the ground is less unstable and the community passes over into the next.

(2) *Dryas* community.

This is more characteristic of the lower, gently sloping regions where the soil is more stable. The result of more favourable soil conditions is the establishment of a more or less closed community in which *Dryas octopetala* is the dominant species, although *Salix polaris* may be co-dominant locally. An important feature is the greater abundance of the mosses due no doubt to the dampness of the soil. The following species have been found in these places, but it must be remembered that all these are not usually present and indeed in some places the *Dryas* has few associates:

| | | | |
|----------------------------|------|--------------------------------|---------|
| <i>Aira alpina</i> | | <i>Pedicularis hirsuta</i> | l. |
| <i>Carex misandra</i> | f. | <i>Polygonum viviparum</i> | o.—f. |
| <i>Cassiope tetragona</i> | l. | <i>Potentilla emarginata</i> | |
| <i>Cerastium alpinum</i> | | <i>Salix polaris</i> | f.—c.d. |
| <i>Draba alpina</i> | | <i>Saxifraga oppositifolia</i> | o.—a. |
| <i>Luzula confusa</i> | o. | <i>Silene acaulis</i> | l.f. |
| <i>Oxyria digyna</i> | | <i>Stellaria longipes</i> | |
| <i>Papaver radiculatum</i> | l.f. | | |

MOSSES.

| | |
|---|---------------------------------|
| <i>Aulacomnium turgidum</i> | <i>Hypnum brevifolium</i> |
| <i>Cynodontium wahlenbergii</i> | <i>Rhacomitrium lanuginosum</i> |
| <i>Dicranum muchlenbeckii</i> | <i>Swartzia montana</i> |
| <i>Hylocomium splendens</i> var. <i>gracilius</i> | |

Lichens also occur but are not very important. *Cassiope* occurs in these districts only in local patches; apparently the climatic conditions for the production of *Cassiope* heath are not present. At the head of Wood Bay no *Cassiope* was seen at all.

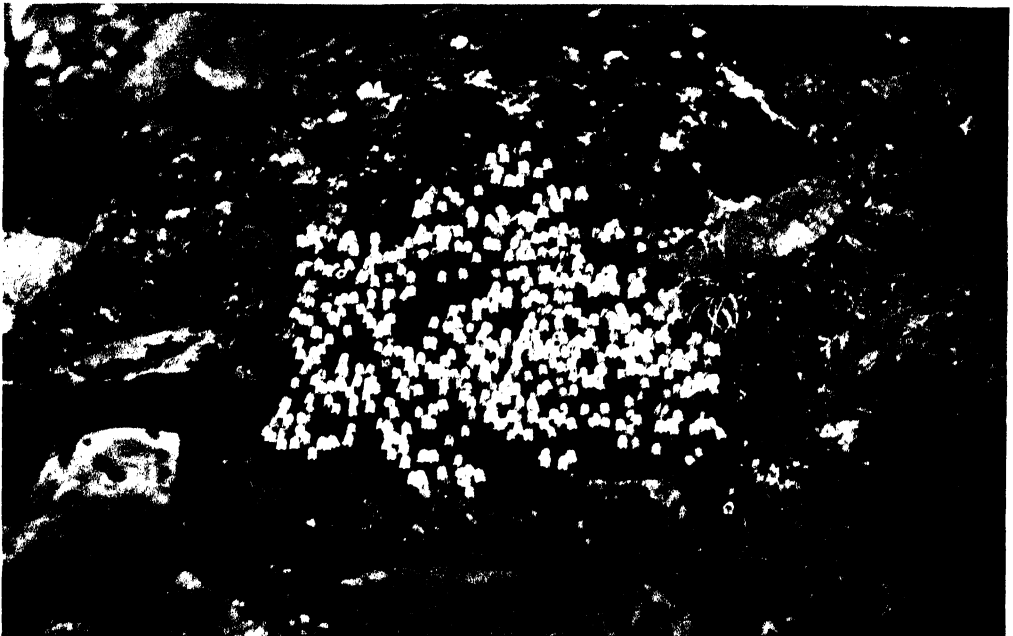
The animal communities of these districts were not investigated thoroughly, but a short visit to the mountains at the base of Reindeer Peninsula showed that the *Dryas* and fjaeldmark animal communities were similar in a general way to those of the Peninsula itself. For instance, in the *Dryas* areas were:

| | |
|--------------------------|--|
| BIRD: | Snow Bunting |
| SPIDER (Araneida): | <i>Leptyphantes sobrius</i> |
| SPRINGTAIL (Collembola): | <i>Isotoma</i> sp. |
| MITE (Acarina): | <i>Rhagidia gelida</i> |
| FLIES (Diptera): | <i>Sciara pallidiventris</i> |
| | <i>Metriocnemus ursinus</i> (aquatic larvae) |

The spider *L. sobrius* and the Snow Bunting are of interest, since they are not found normally on the Peninsula itself, although the Bunting visits it on migration. The reason for their absence is that the conditions are not suitable; as in other parts of Spitsbergen, *L. sobrius* is confined to relatively unstable slopes (see p. 236), while the Snow Bunting nests only in deep crevices among rocks and boulders—a type of habitat which is not produced on Reindeer

*Phot. G. Summers*

Phot. 15. Salmon Lake of Aldert Dirkses Bay (Wijde Bay). The country is composed of granite, gneiss and schists, and is a good example of the "*Cassiope* Zone." On the right can be seen the islands inhabited by terns, which are described on p. 246.

*Phot. J. D. Brown*

Phot. 16. The arctic bell-heather, *Cassiope tetragona*. This species forms heaths at Aldert Dirkses Bay and elsewhere, but is confined almost entirely to the inner parts of the fjords, away from the coast.

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Peninsula, owing to the way in which the rocks weather, and to the isolated nature of the erratic boulders. Another bird seen in the mountains of Liefde Bay and Wood Bay, and not seen on the lowlands, is the Spitsbergen Ptarmigan (*Lagopus mutus hyperboreus*) which feeds on the seeds, leaves, and flowers of the fjaeldmark plants (see Montague, **21**, and Longstaff, **18**).

V. ALDERT DIRKSES BAY DISTRICT (WIJDE BAY).

Aldert Dirkses Bay lies on the east side of Wijde Bay about 10 miles (16 km.) from the entrance, and just south of Mossel Bay, from the hinterland of which it is separated by a glacier-lake 5 or 6 miles (8–10 km.) long, which empties into the sea by a narrow rock-canyon. The New Friesland ice-sheet in this region leaves an ice-free zone along the coast, about 5 to 6 miles (8–10 km.) wide, the rocks of which are granites, gneisses, and schists. This coastal zone is very hilly, the hills rising as shattered rocky knobs among the screes and detritus resulting from their own disintegration, while many lakes and tarns are found scattered over the area (Pl. XXXI, Phot. 15). Granite and gneiss outcrops cover large areas in parts of Spitsbergen, and support a characteristic flora of which the lower plants are especially distinct. We propose therefore to describe the communities at Aldert Dirkses Bay in some detail, and to compare with them other granite and gneiss regions, so far as the flora has been studied. This area also serves as an example of a place enjoying a more favourable climate than that of Reindeer Peninsula, but not so good as that in the interior of the fjords.

The communities in the district may be distinguished as follows:

- (a) Rock and boulder communities.
- (b) Moss-lichen heath.
- (c) Dwarf-shrub heath.
 - 1. *Cassiope* heath.
 - 2. *Empetrum* heath.
- (d) Bogs.
- (e) Aquatic communities.

(a) Rock and boulder communities.

Much of the ground consists of rock outcrops or is covered with a mass of boulders of various sizes. These hard rocks weather but slowly, so that every opportunity is given to lichens and mosses to colonise the surfaces. This colonisation is so effective that rocks previously pink or grey become black from the almost continuous crust of lichens. Foliose lichens are particularly prominent, although no doubt outnumbered, as far as species are concerned, by the crustaceous forms. It was impossible, in the time available,

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to collect the saxicolous lichens at all thoroughly, but the following list gives some idea of the type of community occurring on the rocks:

| | |
|-----------------------------------|--------------------------------|
| Buellia stellatula (on quartzite) | Lecanora tartarea var. frigida |
| Cetraria hepatizon | Lecidea pantherina |
| Gyrophora arctica | *Parmelia alpicola |
| *G. erosa | P. centrifuga |
| *G. hyperborea | P. omphalodes |
| *G. proboscidea | P. pubescens |
| *Haematomma ventosum | *Rhizocarpon geographicum |
| Lecanora polytrpa (on quartzite) | R. grande (on quartzite) |

At North Cape (North-East Land), the granite rocks are similarly covered with lichens, *Parmelia pubescens* being there the most prominent species; others are *Gyrophora erosa* and *proboscidea* and *Lecanora polytrpa*. A number of mosses occur with the lichens, on the rock surfaces, but are never so abundant as the latter; very few were collected at Aldert Dirkses Bay (see below). The following have been recorded from granite and gneiss blocks and rocks in northern Spitsbergen by Berggren (1b): *Andreaea blyttii*, *A. obovata*, *A. papillosa*, *Dicranoweisia crispula*, *Grimmia apocarpa*, *Orthothecium breutelii*, *O. killiasii*, and *O. pellucidum*.

A slope of rock blocks was examined at Aldert Dirkses Bay and gave the following results: on the surface were the lichens marked with an asterisk in the above list, together with the mosses *Dicranoweisia crispula*, *Grimmia apocarpa*, and *Orthothecium killiasii*. Between the blocks were crevices of varying depth. The shallow crevices were occupied by a rich moss and lichen mat, in which were imbedded a few phanerogams, such as *Trisetum subspicatum*, *Saxifraga caespitosa*, *Luzula confusa*, *Draba nivalis*, *Arnica alpina*, etc. The fern *Cystopteris fragilis* was recorded from rock crevices and was not found in other habitats. Other plants were:

| MOSSSES. | |
|--------------------------------|----------------------------------|
| Dicranum elongatum | Hypnum uncinatum |
| Ditrichum flexicaule | Rhacomitrium lanuginosum |
| Hylocomium splendens | Timmia austriaca |
| LICHENS. | |
| Cetraria islandica | Sphaerophorus globosus |
| Cladonia furcata var. palamaea | Stereocaulon paschale and others |
| Dufouria muricata | |

It will be noticed that the fruticose lichens are here the most prominent.

Other mosses have been recorded from similar places in Spitsbergen, those given below being the most characteristic; in some cases they may form the sole flora of the crevices:

| | |
|----------------------------|----------------------------|
| Amblystegium sprucei | Hypnum revolutum |
| Bartramia ithyphylla | Plagiothecium denticulatum |
| Brachythecium trachypodium | Pseudoleskea catenulata |
| Cynodontium polycarpum | Swartzia montana |
| Dicranum blyttii | Tortula ruralis |
| Hypnum polare | |

In deeper crevices the phanerogams are absent, while liverworts become abundant. The following mosses and lichens were found at Aldert Dirkses

Bay, but there are no doubt many more: *Webera cruda*, *Hypnum uncinatum*, *Psoroma hypnorum* var. *deaurata*, and *Lecanora tartarea*.

Grimmia contorta has been found in deep crevices between rocks on Dane's Island and Amsterdam Island (1 b) (compare with similar series on dolerite; and on Bear Island, 29, pp. 225 and 226).

Normally, with the weathering of the rocks the openings become wider and relatively shallower, while soil collects between them and the crevice community gradually passes over to the moss-lichen heath. In this connection it is interesting to note that Isis Point, a small outcrop of granite on the east coast of North-East Land, has only the rock and crevice communities represented, as the recent retreat of the ice-sheet (which still descends to the sea along the rest of the east coast) and the severe climate, have not yet allowed sufficient accumulation of soil to produce moss heath. Thanks to H. W. Florey, we are able to give some notes on the vegetation: *Gyrophora proboscidea* was found on the rocks themselves, while in the crevices were *Ceratodon arcticum*, *C. purpureus*, *Polytrichum hyperboreum*, *P. strictum*, and *Webera nutans*, phanerogams being entirely absent. Isis Point may therefore be considered as an example of the first stage in succession on granite rocks in Spitsbergen.

(b) Moss-lichen heath.

This community is developed extensively at Aldert Dirkses Bay, and seems to replace the fjaeldmark found on other soils, with the exception of dolerite. It occurs on most of the higher parts of the hills, e.g. up to 1000 ft. (300 m.) on "Bird Mountain," being especially developed on the ridges and more open parts, and its distribution is probably connected with the amount and duration of snow covering in the winter and spring. It has been shown before (Lundager, 19, and 29, pp. 201, 279) that *Cassiope tetragona* only forms heaths in places where the snow lies fairly long in spring and is not removed in winter; where these conditions are not fulfilled the *Cassiope* heath is replaced here by *Rhacomitrium* heath or in other districts by fjaeldmark.

In this district the chief constituent of the moss-lichen heath is *Rhacomitrium lanuginosum*, but in contrast to the same community on Bear Island (29, p. 224) lichens are more abundant. Phanerogams occur scattered among the lower plants, but are of little importance, the two most characteristic species being *Luzula confusa* and *Salix polaris*. The plants noted from this community at Aldert Dirkses Bay are given below:

| PHANEROGAMS. | |
|------------------------------|---------------------------------|
| <i>Luzula confusa</i> | <i>Saxifraga caespitosa</i> |
| <i>Potentilla emarginata</i> | <i>S. cernua</i> |
| <i>Ranunculus sulphureus</i> | <i>S. nivalis</i> |
| <i>Salix polaris</i> | and other less frequent species |
| MOSESSES. | |
| <i>Dicranum elongatum</i> | <i>Rhacomitrium canescens</i> |
| <i>Hylocomium splendens</i> | <i>R. lanuginosum</i> d. |
| <i>Hypnum uncinatum</i> | |

LICHENS.

Alectoria ochroleuca
Cetraria cucullata
C. hiascens
C. islandica
C. nivalis
Cladonia degenerans
C. furcata var. *spinosa*
C. furcata var. *palamaea*
C. pyxidata

Dactylina arctica
Dufouria muricata
Haematomma ventosum
Lecanora tartarea var. *frigida*
Parmelia prolixa
Peltigera canina
Sphaerophorus globosus
Stereocaulon alpinum
S. paschale

A characteristic feature of the *Rhacomitrium* heath is the abundance of reindeer horns and dung to be met with, indicating that this area is probably visited by the deer during winter. They are attracted probably by the *Cladonias* and *Cetrarias*, which they can obtain more easily here both because of the abundance of these lichens, and owing to the snow being probably thinner than elsewhere. On the horns were found *Hypnum uncinatum* and *Xanthoria parietina*.

At North Cape (North-East Land), where granite is also the underlying rock, the drier unmanured parts are occupied by a *Rhacomitrium* heath similar to that at Aldert Dirkses Bay, there being here no dwarf-shrub heath, owing to the more severe type of climate. In this area *Stellaria longipes* is abundant, in addition to the *Luzula* and *Salix*, and the phanerogams are altogether more prominent. In places, communities in which *Salix* and *Luzula* are dominant occur, but these only cover small areas. The following list demonstrates the marked resemblances in general character to the Aldert Dirkses Bay community, but also shows the local variation which occurs:

PHANEROGAMS.

| | | |
|---------------------------------------|----------------------------|---------|
| <i>Catabrosa algida</i> | <i>Sagina nivalis</i> | |
| <i>Cerastium alpinum</i> | <i>Salix polaris</i> | f.—c.d. |
| <i>Cochlearia officinalis</i> (small) | <i>Saxifraga rivularis</i> | |
| <i>Draba oblongata</i> | <i>Stellaria longipes</i> | f. |
| <i>Luzula confusa</i> | | f.—c.d. |

BRYOPHYTES.

| | |
|---|---------------------------------|
| <i>Aulacomnium turgidum</i> | <i>Hypnum uncinatum</i> |
| <i>Bryum arcticum</i> | <i>Polytrichum alpinum</i> |
| <i>Cynodontium virens</i> | <i>Rhacomitrium lanuginosum</i> |
| <i>Dicranum bonjeani</i> var. <i>juniperifolium</i> | <i>Webera cruda</i> |
| <i>Hylocomium splendens</i> var. <i>gracilius</i> | |

LICHENS.

| | |
|--|--|
| <i>Cetraria hepatizon</i> | <i>Lecanora tartarea</i> var. <i>frigida</i> |
| <i>C. islandica</i> | <i>Peltigera canina</i> |
| <i>C. nivalis</i> | <i>Psoroma hypnorum</i> |
| <i>Cladonia furcata</i> var. <i>palamaea</i> | <i>Solorina crocea</i> |
| <i>C. pyxidata</i> | <i>Sphaerophorus globosus</i> |
| <i>C. sylvatica</i> | <i>Stereocaulon alpinum</i> |
| <i>Gyrophora polyphylla</i> (on stone) | |

On a reindeer horn in this region was found *Hypnum uncinatum* and *Brachythecium glareosum*. Reindeer dung was also abundant here. Berggren (1 b, p. 24) describes a similar *Rhacomitrium* community from Castren's Island (near North Cape) where it is the chief vegetation on dry stony exposed areas. With it at Castren's Island are *Lophozia alpestris*, *Webera annotina*, *W. cruda*

and *W. ludwigii*, together with many other bryophytes, while *Luzula confusa* ("arcuata") and *Salix polaris* occur sparingly. F. A. Montague, who was with the northern sledging party, noted that *Luzula* was the only important phanerogam on a granite boulder-strewn area near the coast at Extreme Hook, while *Salix* occurred in the form of sparse straggling plants, together with mosses and lichens. The vegetation of this northern granite area of North-East Land appears therefore to be of a fairly definite character; the animals are dealt with earlier on under the Fauna of North-East Land, but we may note here that Montague found horns and old tracks of Reindeer at Extreme Hook.

(c) Dwarf-shrub heath.

1. *Cassiope heath*.

The dwarf-shrub heath at Aldert Dirkses Bay, as in most places in Spitsbergen, is composed almost entirely of the white bell-heather, *Cassiope tetragona* (Pl. XXXI. Phot. 16). This community covers large areas on the lower ground usually up to 200 or 300 ft. (60-90 m.), and is chiefly confined to hollows among boulders and rocky outcrops, where snow lies in the winter. The ground in the summer becomes very dry, as in other *Cassiope* areas. On the ridges and above about 300 ft. (90 m.) it is replaced, as mentioned above, by the *Racomitrium* heath. The most important phanerogam associated with the heather is the dwarf willow, *Salix polaris*, which is dominant in patches locally, while *Dryas octopetala* and *Luzula confusa* are frequent species. The mosses are mainly the same species as those occurring in the *Racomitrium* heath, while white and black encrusting lichens, such as *Lecanora tartarea*, *Pertusaria glomerata*, *Rinodina turfacea*, and *R. conradi*, are abundant on the ground between.

The following is a more complete list of the *Cassiope* heath. It seems to be richer in species than that at Cape Boheman (Icefjord) and elsewhere, but this may be due simply to the greater area covered by the community at Aldert Dirkses Bay.

PHANEROGAMS AND PTERIDOPHYTES.

| | | | |
|-------------------------------|----|--------------------------------|-----------|
| <i>Cardamine bellidifolia</i> | r. | <i>Pedicularis hirsuta</i> | o. |
| <i>Carex misandra</i> | o. | <i>Polygonum viviparum</i> | o. |
| <i>C. parallela</i> | o. | <i>Ranunculus pygmaeus</i> | r. and l. |
| <i>Cassiope tetragona</i> | d. | <i>Salix polaris</i> | l.d. |
| <i>Cerastium alpinum</i> | o. | <i>Saxifraga caespitosa</i> | o. |
| <i>Dryas octopetala</i> | f. | <i>S. cernua</i> | r. |
| <i>Draba lactea</i> | r. | <i>S. nivalis</i> (well-grown) | o. |
| <i>Luzula confusa</i> | f. | <i>S. oppositifolia</i> | o.—f. |
| <i>Oxyria digyna</i> | o. | <i>Silene acaulis</i> | o. |
| <i>Lycopodium selago</i> | o. | <i>Taraxacum nivale</i> | |
| <i>Papaver radicatum</i> | o. | | |

MOSESSES.

| | |
|--|--------------------------------|
| <i>Aulacomnium turgidum</i> | <i>Hylocomium splendens</i> |
| <i>Cynodontium virens</i> | <i>Hypnum uncinatum</i> |
| <i>Dicranum elongatum</i> | <i>Polytrichum alpinum</i> |
| <i>D. bonjeani</i> var. <i>juniperifolium</i> | <i>P. hyperboreum</i> |
| <i>Ditrichum flexicaule</i> var. <i>gracilis</i> | <i>Racomitrium lanuginosum</i> |

LICHENS.

| | |
|--|--|
| <i>Alectoria ochroleuca</i> | <i>Dufouria muricata</i> |
| <i>Candelaria concolor</i> | <i>Lecanora tartarea</i> |
| <i>Cetraria aculeata</i> | <i>L. tartarea</i> var. <i>frigida</i> |
| <i>C. hepatizon</i> | <i>Peltigera aphthosa</i> |
| <i>C. hiascens</i> | <i>Pertusaria glomerata</i> |
| <i>C. islandica</i> | <i>Rinodina conradi</i> |
| <i>C. nivalis</i> | <i>R. turfacea</i> |
| <i>Cladonia furcata</i> var. <i>palamaea</i> | <i>Sphaerophorus globosus</i> |
| <i>C. furcata</i> var. <i>spinosa</i> | <i>Stereocaulon evolutum</i> |
| <i>Dactylina arctica</i> | <i>S. paschale</i> |

The abundance of the lichens is in striking contrast to the paucity of these plants in the Cape Boheman heath, this probably being due to the greater relative humidity of the air at Aldert Dirkses Bay.

In slightly damper regions, the *Cassiope* is replaced by a community the chief constituents of which are *Ranunculus sulphureus*, *Stellaria longipes*, *Saxifraga cernua*, while there is a large amount of *Tortula ruralis*.

On the west side of Bock Bay, an interior arm of Liefde Bay, the rock is schistose, the large scattered boulders often forming slopes as at Aldert Dirkses Bay. These slopes here are occupied by *Cassiope* heath, the accompanying flora again being relatively rich and marked by the abundance of mosses and lichens. Of these, *Rhacomitrium lanuginosum* and *R. canescens* and various species of *Cetraria* are the most abundant, and there seems no doubt that this heath bears the same relation to *Rhacomitrium* heath as at Wijde Bay. In addition to many of the species already given for Aldert Dirkses Bay, the following were found in the *Cassiope* heath at Bock Bay:

| | | | |
|---------------------------|----|--------------------------------|----|
| <i>Potentilla</i> sp. | f. | <i>Draba alpina</i> | r. |
| <i>Pedicularis lanata</i> | f. | <i>Saxifraga hieraciifolia</i> | r. |
| <i>Ranunculus nivalis</i> | o. | | |

Oxyria is much more abundant in this region and grows very luxuriantly, but *Dryas* was not observed, this being an important difference between the communities in the two regions.

MOSSSES.

| | |
|-----------------------------|-------------------------------|
| <i>Camptothecium nitens</i> | <i>Hypnum uncinatum</i> |
| <i>Cynodontium virens</i> | <i>Rhacomitrium canescens</i> |
| <i>Dicranum</i> sp. | <i>R. lanuginosum</i> |

LICHENS.

| | |
|---------------------------|--|
| <i>Cetraria islandica</i> | <i>Lecanora tartarea</i> var. <i>frigida</i> |
| <i>C. nivalis</i> | <i>Psoroma hypnorum</i> |
| <i>Cladonia pyxidata</i> | <i>Rinodina turfacea</i> |
| <i>Dactylina arctica</i> | <i>Sphaerophorus globosus</i> |
| <i>Dufouria muricata</i> | <i>Stereocaulon alpinum</i> |

Since only a hurried visit was paid to Bock Bay, these lists are not to be considered as complete.

The De Geer Range in Adolph Bay at the north of Klaas Billen Bay (Icefjord) consists in its upper parts of gneiss and mica-schist. Here the dominant vegetation is *Cassiope* heath with much *Dryas*, the former being very luxuriant. Other plants occurring here are:

Alsine rubella
Cochlearia officinalis
Draba nivalis
Luzula nivalis
Lycopodium selago
Melandryum apetalum

Pedicularis lanata
Salix polaris
Saxifraga cernua
S. oppositifolia
Woodsia glabella (fern)

This may be looked upon as a particularly luxuriant example of *Cassiope* heath developed in most favourable conditions at the head of a fjord, and on a southerly slope. We are indebted to Mr J. Walton for the notes from this place, made during the 1921 Oxford Expedition.

2. *Empetrum* heath.

The Crowberry (*Empetrum nigrum*) is found only on a south slope in several small patches, which are unmixed at the centre but mixed with *Cassiope* heath at the edges. From the relationships between the two species in northern Scandinavia and Greenland, where *Cassiope* forms heaths at higher altitudes than *Empetrum* (14, p. 92), and the distribution of *Empetrum* in Spitsbergen, we may fairly conclude that *Empetrum* heath takes the place of *Cassiope* heath on such soils as soon as climatic conditions permit, but that owing to the severe climate this stage is only very rarely reached and never over any large area. At Aldert Dirkses Bay H. M. Clutterbuck found one plant with ripe blue-black berries (August 16th), an uncommon occurrence in Spitsbergen, as usually the berries do not ripen. The area occupied by the *Empetrum* heath is not large enough to give any detailed account of the community; it was not found on any of the other gneiss-granite areas studied by us.

The fauna.

The animals of the dry areas can be divided into two communities which do not coincide exactly with the particular plant communities; on the one hand there is the community of comparatively stable ground, which includes the *Cassiope* and *Empetrum* heaths and part of the *Rhacomitrium* heath, while on the other hand that of rather unstable ground, the latter being occupied by *Rhacomitrium* heath, since unstable surfaces occur chiefly on the higher ground.

(1) Stable ground community. Practically all the collecting was done in *Cassiope* heath. The animals were as follows:

| | |
|---------------------------|--|
| MAMMALS: | Arctic Fox Reindeer |
| BIRDS: | Purple Sandpiper Snow Bunting |
| SPIDERS (Araneida): | * <i>Erigone arctica</i> <i>Hilaira glacialis</i> <i>Typhochrestus spetsbergensis</i> |
| MITES (Acarina): | <i>Bdella decipiens</i> <i>Rhagidia gelida</i> <i>Sphaerozetes notatus</i> |
| SPRINGTAILS (Collembola): | <i>Achorutes tullbergi</i> <i>Folsomia quadrioculata</i> <i>Isotoma viridis</i> * <i>Sminthurinus niger</i> |

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FLIES (Diptera):

**Acroptera frontata* (on a warm slope only)
Limnophora hyperborea
L. megastoma
Sciara pallidiventris
S. praecox
S. sp.
 **Trichocera lutea*

WORM (Oligochaeta):

Probably *Henlea brucei*

Those species marked with an asterisk are characteristic of climates better than that of the coast itself. The mites, springtails, and flies were very few in numbers, owing probably to the extreme dryness of the habitat, *Rhagidia gelida* being only common in damper spots, as elsewhere in Spitsbergen. The spiders were very numerous, however, since they had a large additional food-supply in the aquatic flies which fly from the lake close by. At the same time the spiders probably prey on the dry tundra animals also (*Erigone arctica* was seen eating *Rhagidia gelida* elsewhere, 29, p. 262). The following chironomid flies were found by the lake margin, and flying over dry land:

Chironomus lugubris
Cricotopus basalis
 **Orthocladius mixtus*
 **O. trigonalis*

Psectrocladius limbatellus
 **Tanypus barbitarsus*
 **Tanytarsus gracilentus*
 **T. mimulus*

The species marked with an asterisk are lake species which do not occur in shallow ponds.

(2) Community of unstable ground. Here animal life is still more scarce, especially in the upper parts of the hills, away from the water; the only common animals besides the spiders are two mites (*Bdella decipiens* and *Rhagidia gelida*), springtails (*Folsomia quadrioculata*, etc.) and flies (*Sciara*). The chief differences between this and the stable areas is the abundance of the spider *Leptyphantes sobrius*, which is accompanied in places by *Hilaira glacialis*. The restriction of *Leptyphantes* to unstable ground, covered with loose stones and never occupied by closed vegetation, holds good in all the areas in which this spider occurs. In some places (e.g. on Reindeer Peninsula, on Prince Charles Foreland, and at Klaas Billen Bay) it is absent from the flat stabilised lowlands, but is common on the mountain slopes; at Green Harbour, the same relation was found, and it was further noticed that wherever the slope had been stabilised and was occupied by a closed carpet of plants (*Cassiope*, *Dryas*, etc.) *Leptyphantes* was replaced by *Typhochrestus spetsbergensis*, thus showing that stability was the master factor. In the same way, at Aldert Dirkses Bay, *Leptyphantes* is confined to the unstable areas and is replaced at their edges by either *Typhochrestus* or *Erigone arctica*, even on different parts of the same slope. *E. arctica* in this district replaces *E. psychrophila*, which is the common spider on Reindeer Peninsula. *Hilaira glacialis*, like the *Leptyphantes*, tends to come on unstable ground (for example, the two occur together on screes at Advent Bay Valley) but is not completely confined to it.

(d) Bogs.

These communities do not occupy any large areas at Aldert Dirkses Bay, as the lakes mostly have rocky banks, so that little fringing bog is developed. Where the drainage is bad, bogs may occur with standing water, and here *Eriophorum scheuchzeri* is the most prominent species of phanerogam. In other places *Salix polaris* is found, associated with mosses, together with a number of fungi.

Small fringing bogs are often found by streams, mosses again predominating: in one such bog, *Saxifraga cernua*, *S. rivularis*, and *Stellaria longipes* occurred, together with the mosses *Aulacomnium palustre*, *Brachythecium latifolium*, *Bryum obtusifolium*, *Hypnum sarmentosum*, and *Polytrichum alpinum* var. *septentrionale*. In similar stream bogs at Bock Bay, *Saxifraga stellaris* var. *comosa* occurs in the mossy carpet, which includes among other species *Hypnum sarmentosum* var. *fallaciosum* and *H. revolvens*.

At North Cape *Arctophila fulva* is a prominent constituent of bogs, but these were not studied in detail. We have no data about the animals of the bogs at Aldert Dirkses Bay.

(e) Aquatic communities.

The most striking feature of this district is the large number of very varied and beautiful lakes and tarns (Pl. XXXI, Phot. 15), whose fauna would be well worth investigating more fully, but was not carefully studied by us owing to lack of time. Salmon Lake is devoid of submerged vegetation (as are all the others), with the exception of large masses of green filamentous algae in the shallow littoral zone. The larvae of chironomid flies are abundant and probably form the chief food of the Spitsbergen Char (*Salmo umbla stagnalis*), which comes up from the sea to such lakes in order to breed, and in some cases appears to live in them permanently. The stomach of the only one caught by us in Salmon Lake contained about three hundred larvae and pupae of chironomid flies. Besides these flies (listed above on p. 236), a species of Caddis-fly (*Goniotaulus arcticus*) has been recorded from Aldert Dirkses Bay by Boheman (3).

Red-throated Divers (*Colymbus stellatus*) are common, and the Great Northern Diver (*Colymbus immer*) also occurs, this being its only known station in Spitsbergen. These two birds, together with Mandt's Black Guillemot (*Uria grylle mandtii*), which is normally a sea-bird, but here frequents fresh-water, presumably fish for the arctic Char. Arctic Terns nest on the islands in Salmon Lake, and have produced peculiar plant and animal communities by their manuring (see p. 246).

VI. NITROPHILOUS COMMUNITIES.

The supply of available nitrogen in the soil is very small in arctic regions, owing to the low temperatures throughout most of the year, and the consequent scarcity of soil bacteria and fungi. It follows, therefore, that whenever the supply of available nitrogenous (and perhaps also phosphatic) materials is above the normal, an unusually rich and luxuriant vegetation is produced. In these communities the dominant and abundant species are normally those which, although present in other communities, are yet of little importance there, while a few species are restricted to such nitrogen-rich areas. The most striking feature of the nitrophilous communities is the abundance of *grass*, which is always scarce in other habitats, but here is usually the dominant type of vegetation.

There are two chief ways in which the increase of nitrogen may take place: namely (1) manuring by birds and animals, and (2) the deposition of refuse around settlements by man. The second of these is of little importance in Spitsbergen, mainly because the areas around settlements have been altered by many other human influences and the resulting communities may not always be due simply to increase of nitrogen. Owing to the varied nature of the factors producing these communities, they tend to show no definite character, but to resemble the ruderal communities of this country. However, it is suggestive that many of the plants found commonly around settlements are the same species as those which are so prominent under bird-cliffs. As a matter of fact, since there are only a few settlements in Spitsbergen, the area influenced by them is extremely small.

Communities produced by the manuring of birds, especially sea-birds, occur very frequently in Spitsbergen and are often of quite considerable extent. They may be divided into two chief classes. The majority of the sea-birds of Spitsbergen nest on cliffs which are usually on the coast, but which may sometimes occur far inland. The dung deposited by the birds affects not only the cliffs themselves but usually the scree which almost invariably occurs below them, and often, although to a lesser extent, some of the flatter ground lying beyond. The nitrophilous communities occurring in these habitats may be included in a "Cliff Series." The chief birds involved in this series are Guillemots, Kittiwakes, Puffins, Fulmar Petrels, and Little Auks. Other birds, however, nest either on flat areas or among rocks, but not on cliffs, the more important of these being Eider Ducks, Arctic Terns, and Skuas. The plant communities in these cases, although of the same general character as those below cliffs, may be quite different in detailed floristic composition, and obviously the characters of the habitat are very different. This series of communities can be conveniently termed the "Non-cliff Series."

We have already, in our previous paper, given some examples of both these types of community (see 29, pp. 218, 223, 237, 277, 280, 281). During



Phot. T. G. Longstaff

Phot. 17. North Cape, North-East Island (height about 450 feet = 135 m.). The darker patches on the screes represent the richer vegetation produced by the manuring of birds (Little Auks, etc.) which nest on the granite cliffs above.



Phot. A. N. T. Rankin

Phot. 18. The Alkrange, a huge bird-cliff in Hinlopen Strait, the birds on the ledges are Brünnich's Guillemots (*Uria lomvia lomvia*), while above them can be seen Glaucous Gulls (*Larus hyperboreus*), sitting on the pinnacles of dolerite.

SUMMERHAYES & ELTON—FURTHER CONTRIBUTIONS TO THE
ECOLOGY OF SPITSBERGEN

1923 and 1924 several cases were examined in which the birds responsible were different from those dealt with in 1921, while the climatic conditions were quite distinct. It has therefore been thought useful to give the results. Some of the communities are particularly striking, as they form oases of green vegetation in some of the most desolate and barren regions of the archipelago.

(a) **Cliff series.**

Examination of records shows that the various cliff-dwelling sea-birds may be associated in many different ways as far as nesting is concerned. There seem, however, to be two distinct types of sea-bird colonies, namely, large ones in which Brünnich's Guillemots occur in immense numbers, together with Kittiwakes (Pl. XXXII, Phot. 18); and small ones in which the birds are Little Auks, Mandt's Guillemots, or Northern Puffins, or various combinations of these (Pl. XXXII, Phot. 17). Glaucous Gulls may be associated with any or all of these. The only other types of colony are those formed by Fulmar Petrels and by Ivory Gulls. The Fulmar Petrel usually nests away from the sea-coast, either at the heads of the fjords, or else on inland nunataks. The Ivory Gull occurs in two large colonies on the south side of Wahlenberg Bay, and at Cape Torell—both places being near the ice-pack, where this bird finds its food. With the Ivory Gull, Kittiwakes are also generally found. It has not been possible to correlate the presence of any particular species of bird with any special change in the flora: the data necessary for this purpose would probably take years to collect. There are however definite variations in the nitrophilous vegetation, associated with the general climatic zones in the archipelago. In our previous paper (29, p. 277) we pointed out the differences between the bird-cliff floras of Sassen Bay (in Icefjord) and Prince Charles Foreland. Extension of the study to north-eastern Spitsbergen with its more severe climate confirms these observations, but shows in a rather remarkable manner that the differences lie in the number of species rather than in the actual dominants.

Lists from eight different localities on the north and east coasts show that the following are the most prominent species on the screes below the cliffs:

Saxifraga cernua, *S. caespitosa*, *S. rivularis*, *Cerastium alpinum*, *Cochlearia groenlandica* and *C. arctica*, *Papaver radiculatum*, *Alopecurus alpinus* and *Catabrosa algida*.

These are the characteristic plants for similar localities in Icefjord. However, in the fjords many species are present which only occur rarely, if at all, in the north and east. The distribution and abundance of these species then follow the climatic zones, and are not determined by the extra nitrogen available. It is therefore most probable that such plants as *Polemonium humile* are restricted to warm sunny slopes rather than to manured areas, the two characters often being combined in nature. Possibly some species require

both factors for existence in Spitsbergen. The maintenance of similar communities bearing the same dominants, cutting right across the zonation produced by climate, shows how paramount is the effect of lack or presence of nitrogen in the Arctic. Examination of charts of the distribution of certain species suggests that they may occur in the localities with more extreme climate only as far as bird-cliffs are present, e.g. *Ranunculus pygmaeus*, *Alopecurus alpinus*, *Potentilla emarginata*, and *Saxifraga hieraciifolia*. This seems to apply also to some of the lower animals, although very few collections were made on bird-cliff screes. At Cape Eremit (Hinlopen Strait), the normal fjaeldmark and moss-lichen heath were almost devoid of animal life, but on a north slope below cliffs inhabited by Mandt's Guillemots and Glaucous Gulls, three species of mites (*Bdella littoralis*, *B. decipiens*, and *Rhagidia gelida*) and a spider (*Typhochrestus spetsbergensis*) were numerous, while a similar better fauna was found on skua hummocks on the flatter areas (see p. 242).

Our data on the flora of the cliff surfaces and ledges is very incomplete owing to their inaccessibility. In addition to *Alopecurus* and *Cochlearia* and other phanerogams, which may often be recognised through field-glasses, the rocks in all localities have a more or less continuous covering of orange or reddish lichens. The following have been identified from such places, but with careful search many more should be found:

Caloplaca elegans
Physcia muscigena
Parmelia pubescens

Locanora frustulosa
Xanthoria lychnaea var. *pygmaea*

Of these, *Caloplaca elegans* seems the most prominent.

On the slopes, the vegetation tends to be very varied, depending upon the stability of the slope, and the concentration of the nitrogenous material. The vegetation is however usually closed, although it may be quite open in places and here is really a type of fjaeldmark. The various degrees of closeness of the covering are to be interpreted as different stages in a succession from bare scree to a stabilised slope, the manuring enabling this to take place at an increased rate, and more effectively. The final stage, which is not necessarily always reached, is a grass-turf formed of various species (e.g. *Poa alpina*, *P. abbreviata*, and *P. arctica*); such grass-turf is not found in Spitsbergen in dry places outside nitrophilous areas. The luxuriance of these grassy slopes is shown by some comparisons made with a standard colour chart. The grassy or herbaceous slopes on the hillsides of Tromsø Fjord in Norway matched green "no. 20" on the chart; at Green Harbour, in Spitsbergen, the slopes below bird-cliffs were the same colour, while the general fjaeldmark on the other slopes matched brown "no. 41." (For these observations we are indebted to Mr R. A. Frazer.)

In addition to the closed character of the vegetation, the luxuriance of the plants is also often very striking. Many species, e.g. *Saxifraga cernua*, *Cochlearia* spp., and *Ranunculus sulphureus*, which in the normal fjaeldmark



Phot. C. S. Elton

Phot. 19. The effect of increased nitrogen supply on plants: specimens of *Catabrosa algida* collected from dolerite rocks at a height of 4000 feet on Mount Scott-Keltie (at the bottom of Wood Bay). The large plant on the right was growing on manured soil below the nesting place of a Fulmar Petrel. The small one on the left was growing on an unmanured spot.

or other non-nitrophilous communities are relatively small, develop into plants 6–12 in. (15–30 cm.) high, under bird-cliffs. Plate XXXIII, Phot. 19, shows specimens of *Catabrosa algida* which illustrate this point.

Mosses are often more abundant than phanerogams, very many species being found in such communities (see Berggren). The more prominent ones seem to be *Tortula ruralis* and *Brachythecium salebrosum* var. *arcticum*, although the bryophyte flora is very rich and varied. A number of species are especially characteristic of such places, and indeed are rarely found outside them, e.g. *Ceratodon purpureus*, *Orthothecium breutelii*, *Webera* spp., *Splachnum* spp., etc. At Lomme Bay below a limestone cliff, inhabited by nesting Puffins, a closed community dominated by *Saxifraga oppositifolia* was observed, this being very exceptional; while at Aldert Dirkses Bay, on a slope below a Glaucous Gull colony and facing south-west, the most abundant plant was *Polygonum viviparum*, there being also here plants of *Ranunculus sulphureus* up to 10 in. (25 cm.) in height, while *Poa arctica* was the most abundant grass. These communities are floristically rather closely related to the various "Wiesen" described by Fries in northern Scandinavia (12, pp. 110–120) (particularly the "*Polygonum viviparum* Wiesen"), but are very much poorer in species. In each case a fresh, rather rich soil is important, but in Scandinavia manuring is a negligible factor in producing the community.

(b) Non-cliff series.

There are two main types of community of this sort, namely, "skua hummocks," and "bird islands." We have already described the skua hummocks in Bear Island (29, p. 223) where in certain barren districts they are a very prominent feature in the landscape; they were encountered in similar country at Cape Eremite in Hinlopen Strait. They are typically grass-covered mounds rising slightly above the normal surface of the rather open fjaeldmark. One at Cape Eremite was 2 to 3 ft. (0.6 to 0.9 m.) high and about 10 to 15 ft. (3 to 4.5 m.) long. A close turf of *Poa alpigena* is characteristic of the summit of the mounds, while other important phanerogams are *Alopecurus alpinus*, *Cerastium alpinum*, *Stellaria longipes*, and *Potentilla emarginata*, all but the *Stellaria* being plants generally associated with increased nitrogenous supply. *Cochlearia arctica* also occurs. The list at Cape Eremite is much longer than that at Bear Island, and this is probably correlated with the richer flora of Spitsbergen, and not with any superiority of the climate or habitat.

As an example of how the flora of a similarly produced community may vary from place to place, a list of the cryptogams found on skua hummocks at Cape Eremite, is given for comparison with the one for Bear Island skua hummocks given in our other paper (29, p. 223):

BRYOPHYTES.

On drier parts:

Aulacomnium palustre
Brachythecium salebrosum var. *arcticum*
Bryum obtusifolium

Ceratodon purpureus
Hypnum uncinatum
H. sarmentosum
Philonotus tomentella

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| | |
|------------------------|---------------------------------------|
| Polytrichum alpinum | Dicranum bonjeani var. juniperifolium |
| Rhacomitrium canescens | Ditrichum flexicaule var. densum |
| Tortula ruralis | Haplodon wormskjoldii |
| On damper parts: | Polytrichum sp. |
| Aulacomnium palustre | Webera nutans and many hepatics |
| Dicranum elongatum | |

LICHENS.

| | |
|--------------------------------|----------------------|
| Cetraria nivalis a. | Cladonia lepidophora |
| C. islandica | Stereocaulon alpinum |
| Cladonia furcata var. palamaea | |

The remarkable fact which emerges is that *Tortula ruralis* and *Hypnum uncinatum* are the only plants common to the two lists.

As mentioned above, the skua hummocks at Cape Eremitte had a certain number of animals not found in the surrounding fjældmark. These include a springtail (*Achorutes viaticus*), a mite (? *Bdella* sp.), a land-fly (*Sciara* sp.), and probably spiders. In addition they were visited by certain aquatic flies,

| | | | | | Hummock Centre | Margin | Normal Fjældmark |
|--------------|--|-----|-----|-----|-------------------|---------|---------------------|
| PHANEROGAMS: | Cardamine bellidifolia | ... | ... | ... | — | r. | — |
| | Poa sp. | ... | ... | ... | o.—f. | a.—l.d. | — |
| | Cerastium alpinum | ... | ... | ... | o.—f. | f. | o. |
| | Draba sp. (white flowered) | ... | ... | ... | — | o. | — |
| | Luzula confusa (small) | ... | ... | ... | f. | a. | a. |
| | L. confusa (large) | ... | ... | ... | — | a.—l.d. | — |
| | Oxyria digyna | ... | ... | ... | r. | f. | — |
| | Papaver radiculatum | ... | ... | ... | — | o. | o.—f. |
| | Salix polaris | ... | ... | ... | — | o.—f. | c.d. |
| | Saxifraga caespitosa | ... | ... | ... | — | — | o. |
| | S. cernua | ... | ... | ... | — | o. | — |
| | S. nivalis | ... | ... | ... | — | o. | o |
| | S. oppositifolia | ... | ... | ... | — | — | o. |
| | S. rivularis | ... | ... | ... | — | o. | — |
| | Stellaria longipes | ... | ... | ... | a. | o.—f. | — |
| LICHENS | ... | ... | ... | ... | f. | o.—f. | c.d. |
| | Alectoria oehroleuca | ... | ... | ... | — | — | x |
| | Cetraria islandica | ... | ... | ... | — | — | x |
| | C. nivalis | ... | ... | ... | r. | r. | a. |
| | Cladonia spp. | ... | ... | ... | o. | o. | o. |
| | C. uncialis | ... | ... | ... | x | — | — |
| | Dufouria muricata | ... | ... | ... | — | — | o. |
| | Lecanora tartarea var. frigida | ... | ... | ... | x | x | c.d. |
| | Lecidea arctica | ... | ... | ... | — | x | — |
| | Rinodina turfacea | ... | ... | ... | x | x | c.d. |
| MOSSES | Sphaerophorus globosus | ... | ... | ... | o. | o. | o. |
| | ... | ... | ... | ... | d. | a.—l.d. | f. |
| | Aulacomnium palustre | ... | ... | ... | x | x | — |
| | A. turgidum | ... | ... | ... | x | — | — |
| | Brachythecium salebrosum var. arcticum | ... | ... | ... | — | x | — |
| | Camptothecium nitens | ... | ... | ... | — | x | — |
| | Dicranum groenlandicum | ... | ... | ... | — | x | — |
| | D. flexicaule | ... | ... | ... | x | x | x |
| | D. f. var. densum | ... | ... | ... | x | — | — |
| | D. f. forma | ... | ... | ... | — | — | x |
| | Hypnum revolutum | ... | ... | ... | — | — | x |
| | H. uncinatum | ... | ... | ... | x | x | x |
| | Polytrichum spp. | ... | ... | ... | a.—d. | f.—a. | o.—f. |
| | P. alpinum | ... | ... | ... | — | x | No sample |
| | P. strictum | ... | ... | ... | x | — | No sample |
| | Timmia austriaca | ... | ... | ... | — | x | — |
| | T. austriaca var. arctica | ... | ... | ... | — | x | x |
| | Webera cruda | ... | ... | ... | x | — | x |
| | W. nutans | ... | ... | ... | x | x | — |
| | Number of species | ... | ... | ... | 19 | 30 | 22 |



Phot. A. N. T. Rankin

Phot. 20. Arctic Tern (*Sterna macrura*) on its nest on one of the Station Islands, Liefde Bay. The moss-lichen mat formed by the manuring of the birds can be seen.



Phot A. N. T. Rankin

Phot. 21. Brent Goose (*Branta bernicla hrotah*) on its nest on one of the Station Islands, Liefde Bay. This bird is occupying the grassy patches produced by the manuring of Arctic Terns, a habitat upon which the Terns themselves refuse to nest.

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probably breeding in stream-bogs close by, viz. *Trichocladius lustralis*, *Camptocladius pumilio*, and *Metriocnemus obscuripes*.

A large skua hummock dominated by *Luzula*, grass, and mosses was also seen on Reindeer Peninsula, this one being 25 ft. (7.5 m.) in diameter and 6 to 12 in. (0.15–0.3 m.) high. The hummock was frequented by Reindeer which had added their dung to that of the Skuas. An interesting vegetation gradient from the normal fjaeldmark outside to the manured centre was noticed and the zones are listed on p. 242.

It will be noticed that there are more species on the margins of the hummocks than either in the centre or on the surrounding dry fjaeldmark. This is explained probably by the severe competition on the manured centre on the one hand, and by the pooriness of the fjaeldmark soil on the other. The frequencies of the lichens support the general opinion that these plants, with the exception of a few species, are not favoured by increased nitrogenous supply. As is usually the case, the lower animals were much more abundant on the centre and margins of the closed community than on the fjaeldmark around, but the species are the same:

| | |
|--------------|---|
| SPIDER: | <i>Erigone psychrophila</i> |
| MITES: | × |
| SPRINGTAILS: | <i>Folsomia 4-oculata</i> <i>Onychiurus armatus</i> var. <i>arcticus</i> <i>Achorutes</i> sp. |
| FLIES: | <i>Psectrocladius limbatellus</i> (from neighbouring tarn) |
| WORMS: | × |

Bird islands.

In this category are included all islands which support a large community of ground-nesting birds, of which the commonest species are Northern Eider Ducks (*Somateria mollissima borealis*) and Arctic Terns (*Sterna macrura*) (Pl. XXXIV, Phot. 20), while others are the Brent Goose (*Branta bernicla hrotah*) (Pl. XXXIV, Phot. 21), Pink-footed Goose (*Anser brachyrhynchus*), Long-tailed Duck (*Harelda glacialis*), King Eider Duck (*Somateria spectabilis*), Red-throated Diver (*Colymbus stellatus*), and the Grey Phalarope (*Phalaropus fulicarius jourdaini*). Sabine's Gull (*Xema sabini*) occurs locally, while birds of the normal fjaeldmark, such as the Skua, Purple Sandpiper, and Snow Bunting, are also found. The Eider Ducks are harassed by the Arctic Skua which sucks their eggs; but the Arctic Tern, owing to its fierce nature, is immune. The Eider Duck, Arctic Tern, and Brent Goose, together with Sabine's Gull, are usually confined to such islands since they are there free from the depredations of the Arctic Fox (*Canis lagopus*). The Pink-footed Goose nests also on the mainland, because its larger size enables it to drive off foxes; in the summer of 1924 we actually watched a fight between a fox and a Pink-footed Goose, on the shore of Cape Roos. The fight resulted in a victory for the goose; but on the approach of our party the goose fled and the fox was then able to run off with one of its eggs.

The continuous manuring (and in the case of Eiders, trampling) results in a modification of the flora, producing quite different communities from those on the adjoining mainland. Two very good examples of this were worked out—on the Station Islands in Liefde Bay, and on some small islands in Salmon Lake at Aldert Dirkses Bay. The vegetation in the two cases agrees, in that the effect of the manuring has been to change the course of succession towards a climax of grass-turf (*Poa alpigena* and *P. arctica*), instead of dwarf-shrub heath. In both these cases the chief birds are Terns, but Eider Ducks also occur on the Station Islands, and on the Eastern Island they predominate. The communities found may best be treated as stages in a succession from bare rock to closed grass-turf.

Station Islands. Here the rock, which is a red shale, is plentifully covered with lichens, of which the following were collected: *Caloplaca elegans*, *C. murorum*, *Lecidea lithophylla*, and *Rhizocarpon geminatum*. The rock weathers easily to a produce a gravelly mud which later dries and cracks into polygons. The centres of the polygons are occupied at first by lichens only, the common ones being *Physcia muscigena* and *Lecanora tartarea* var. *frigida*. As the lichens cover the ground more closely, they are invaded by mosses, of which the most important species are *Tortula ruralis*, *Brachythecium salebrosum* var. *arcticum*, and *Swartzia montana* var. *compacta*, together with such species as *Encalypta rhabdocarpa*, *Pottia heimii*, and *Hypnum vaucheri*. The first two, it will be recalled, are the most important mosses below bird-cliffs.

Simultaneously with the lichen invasion of the polygon centres, appear various phanerogams in the cracks between, and as the whole area becomes covered with vegetation these spread on to the centres. *Poa* spp. soon arrive, there being associated with them:

| | | | |
|---|-------|-----------------------------|------|
| <i>Alsine rubella</i> | f. | <i>Salix polaris</i> | l.a. |
| <i>Cerastium alpinum</i> | f. | <i>Saxifraga caespitosa</i> | l.f. |
| <i>Cochlearia</i> | f.—a. | <i>S. cernua</i> | r.—o |
| <i>Festuca rubra</i> var. <i>arenaria</i> | | <i>S. rivularis</i> | l. |
| <i>Potentilla emarginata</i> | a. | <i>Silene acaulis</i> | l.a. |
| <i>Sagina nivalis</i> | | | |

Before the actual climax itself is reached there is a stage in which *Saxifraga caespitosa* is abundant; but as the *Poa* increases in amount, most of the other phanerogams are eliminated, *Hypnum uncinatum* alone remaining constantly associated with the grass. However, local patches dominated by *Salix polaris*, *Dryas*, and *Saxifraga oppositifolia* may be found, and may be interpreted as areas where the manuring effect is not so intense. These indicate the possible line of succession in the absence of manuring. *Dryas* heath then being one of the climaxes.

Below the grass-turf there was a layer of peat 6 in. (15 cm.) or more in thickness, with a thin black layer at the base, this probably representing the earlier lichen layer. Other mosses occurring in the grass-turf are *Brachythecium*

salebrosum var. *arcticum*, *Mnium affine* var. *integrifolium*, *Swartzia montana*, *Timmia austriaca*, and *Tortula ruralis*.

The Terns have a definite system of nesting territory which results in the sitting birds being spaced out at an average distance of about 40 ft. (12 m.) from one another, the actual distances varying from 30 ft. (9 m.) to 70 ft. (20 m.). It is interesting to note that in the exceptional case of one bird which was only 12 ft. (3.5 m.) from its neighbours, the nesting materials consisted of pieces of dung instead of the usual small stones or shell-fragments, indicating an abnormal mentality. Each bird defends its own territory from all intruders with great ferocity; at the same time the Terns in making their nests show well-marked preferences for certain types of ground, but owing to their strict system of territory the choice of habitats is usually limited for any one bird.

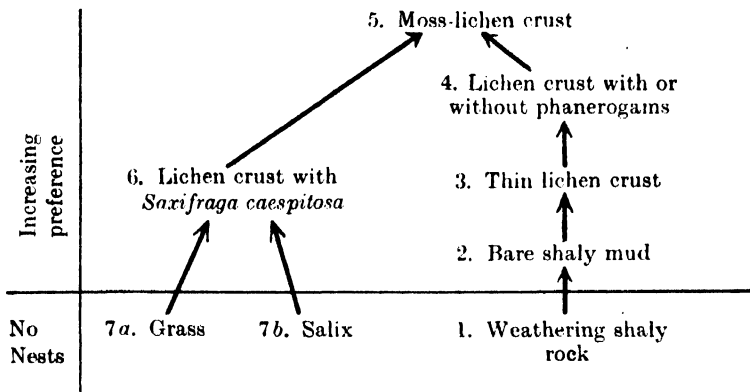


FIG. 5. Scale of preferences for different nesting sites shown by Arctic Terns on the Station Islands, Liefde Bay. The arrows point to the type of habitat more preferred; the numbers refer to the stages in succession from bare rock to a climax. It will be seen that the middle stage of succession is the one most preferred.

By compiling a list of the types of ground chosen by each bird *from those available within its nesting territory*, it was possible to work out the complete scale of preferences in this matter, and this is shown in Fig. 5.

There were only a few Terns nesting on the bare shaly mud areas around the coast, but where one did occur, the bird always selected the least bit of lichen or moss-covered ground, and all equally avoided the turf or *Salix* climax communities. These grassy areas, however, attract the Brent Goose, which nests and feeds there, Phalaropes also being found. Since the Terns are the sole factor producing the grass-turf, they are bringing about conditions which would eventually drive them off the island, but which would make it possible for Brent Geese to exist in increasing numbers.

In the grass-turf is found a community of lower animals which is considerably better developed, both in species and individuals, than that of the tjaeldmark on the mainland.

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| | |
|---------------------------|--|
| SPIDERS (Araneida): | <i>Erigone psychrophila</i> <i>Typhochrestus spetsbergensis</i> |
| MITES (Acarina): | <i>Bdella decipiens</i> <i>Halotydeus insulanus</i> <i>Penthaleus</i> sp. <i>Sphaerozetes notatus</i> a. |
| SPRINGTAILS (Collembola): | <i>Achorutes longispinus</i> o. <i>A. viaticus</i> o. <i>Folsomia 4-oculata</i> a. <i>F. fimetaria</i> a. <i>Onychiurus groenlandicus</i> a. |
| BRACONID (Hymenoptera): | A species of braconid |
| FLY (Diptera): | A small species of ? <i>Sciara</i> |
| WORM (Oligochaeta): | <i>Henlea brucei</i> |

The resemblance of this list to that of the skua hummock given above is interesting, also the absence of chironomid flies, due to the fact that there are no ponds on the island from which the collection was made. The braconid may be parasitic on the land-fly and certainly not on any chironomid. Many of the animals occurred also in the thick *Hypnum uncinatum* mats containing *Salix polaris*.

Tern Islands, Salmon Lake, Aldert Dirkses Bay (Pl. XXXI, Phot. 15). The islands are very small, not exceeding 30 ft. (9 m.) in diameter, and are occupied in summer by a nesting colony of Arctic Terns, which have produced striking effects on the vegetation. One island, about 30 ft. (9 m.) across, was worked out in great detail. Since it was composed of gneiss and schists, it supported an abundant and varied lichen flora, and the following species were obtained from the rock surface:

| | |
|--|---|
| <i>Acarospora fuscata</i> var. <i>flavescens</i> | <i>L. upsaliensis</i> |
| <i>A. veronensis</i> | <i>Lecidea auriculata</i> |
| <i>Buellia crispa</i> | <i>Rhizocarpon geographicum</i> |
| <i>Dermatocarpon minutum</i> | <i>Rinodina melvina</i> |
| <i>Lecanora sordida</i> var. <i>inflexa</i> | <i>Xanthoria lychnaea</i> and var. <i>pygmaea</i> |

Invasion of the weathering rock by higher plants takes place primarily in the cracks. The grass *Catabrosa algida* is the chief plant to appear at first, and is accompanied by thick seams of the green alga *Prasiola crispa*. Enormous numbers of the scarlet mite *Bdella littoralis* were living among the lichens and alga, and the young mites were apparently feeding on the latter. Under the mats of *Catabrosa* were large numbers of a white springtail *Onychiurus armatus* var. *arcticus*, whose eggs were laid in groups on the damp rock surface. The vegetation gradually spreads outwards from the cracks, until finally a solid turf of *Poa alpigena* and *P. arctica*, 6 in. (15 cm.) or more in thickness is formed, with which are *Salix polaris*, *Saxifraga oppositifolia*, *Cerastium alpinum*, *Luzula confusa*, and a large amount of *Tortula ruralis*. Other phanerogams occurring more sparingly are *Saxifraga caespitosa*, *S. cernua*, *Draba lactea*, *Carex parallela*, and *Aira alpina*. Small patches of *Dryas* and *Cassiope* indicate the normal climaxes to the succession, which would be reached everywhere if the manuring were not so intense.

In damper parts of the islands the grass-turf is replaced by a rich, dense, moss community, with plants of *Saxifraga rivularis* and *Chrysosplenium tetrandrum*. The mosses found are as follows:

| | |
|----------------------------------|--------------------------|
| Aulacomnium palustre | Hypnum stramineum |
| Cynodontium virens var. arcticum | H. uncinatum |
| C. wahlenbergii | Rhacomitrium lanuginosum |
| Dicranum elongatum | Tortula norvegica |
| D. bonjeani var. juniperifolium | Webera nutans |
| Haplodon wormskjoldii | |

With the exception of the *Haplodon*, this list does not show very markedly the effect of manuring.

The animals of the turf climax were as follows:

| | |
|---------------------------|--|
| SPIDER (Araneida): | Typhochrestus spetsbergensis |
| MITES (Acarina): | *Bdella littoralis |
| | *Bryobia praetiosa |
| | *Cyta brevirostris |
| | *Gamassellus borealis |
| | Rhagidia gelida |
| SPRINGTAILS (Collembola): | Achorutes tullbergi |
| | *Onychiurus armatus var. arcticus |
| FLIES (Diptera): | Cricotopus basalis and other chironomids from the lake |

Under large flat stones were found

| | |
|---------------------------|----------------------|
| SPIDER (Araneida): | Leptyphantus sobrius |
| MITE (Acarina): | Bdella decipiens |
| SPRINGTAILS (Collembola): | Isotoma viridis |
| | Sminthurinus niger |

Those species marked with an asterisk were not recorded from the normal dry communities on the mainland. *Bdella littoralis*, properly a sea-shore species, probably reached these islands on the feathers or feet of the Terns.

At Reindeer Peninsula there is an interesting type of special nitrophilous community developed just above the drift-line on the edge of the coastal fjaeldmark. Eider Ducks stand here with their families, during intervals between fishing for molluscs in the adjacent water, and their dung affects a narrow strip of ground. *Cochlearia groenlandica* is particularly abundant in the zone, while *Catabrosa algida* is a common grass, which is eaten a good deal by the ducks.

Conclusion. The chief point of importance in connection with the nitrophilous communities in Spitsbergen lies in the effect of the increased nitrogen on the succession of communities. Normally this passes from bare rock through fjaeldmark up to dwarf-shrub heath of *Dryas* or *Cassiope*, according to the climate. The manuring by birds deflects this "Heide" or heath series into what may be properly termed a "Wiesen" series, in which the climax is a herb or grass community on a fresh neutral soil. The addition of elaborated nitrogenous food directly to the plants therefore results in the production in the Arctic of communities similar to those which occur in more temperate countries on soils capable of considerable nitrification, i.e. on the whole, neutral or alkaline soils. This is what might have been expected.

There is another striking thing about the nitrophilous communities we have described: they show in a very clear way how plant life is affected by animals, which have themselves drawn their food-supply from the sea, through a long chain of animals, which in turn depend ultimately on marine diatoms for their basic food-supply. These effects on the terrestrial plants have a further influence on the lower forms of land animals, which are in most cases better able to maintain themselves in a closed grass community than in the dry fjaeldmark or heaths. It is plain therefore, that the distribution and numbers of mites like *Bryobia practiosa* are indirectly but effectively dependent upon the quantity and quality of marine plankton diatoms in the arctic seas.

VII. MARITIME COMMUNITIES.

The animals and plants which live on or near the sea-shore in Spitsbergen are few in number; but as they illustrate rather well the gradient in climate which is also shown by the terrestrial animals and plants, we are giving a brief description of them here. They may be divided into three types of community:

1. Intertidal.
2. Drift-line.
3. Scavengers in dead animals.

1. INTERTIDAL.

The communities in intertidal areas may again be divided into three, those of rock, shingle, and mud.

(a) Rocky coasts.

In those regions which are constantly under the influence of the ice-pack in summer, there is absolutely no life at all between tide-marks; in fact even the drift-line community is almost absent. Two species of intertidal animal do occur here, living, however, not between tide-marks, but on the land, either at the drift-line or a little way above it (as in the case of the worm *Lumbricillus aegialites*) or actually on the fjaeldmark (as in the case of the mite *Bdella littoralis*).

In regions free from ice in summer the conditions between tide-marks are better. On the shores of Liefde Bay, the grinding action of ice in autumn and spring, and the cold climate, discourage the growth of sea-weeds in most places, but these do occur locally. *Fucus evanescens* occurs fairly abundantly in a few places between tide-marks on the south side of Reindeer Peninsula, accompanied locally by *Pylaiella littoralis* or *Enteromorpha compressa*. The amphipod *Gammarus locusta* occurs where there is *Fucus*, while *Bdella littoralis* and the springtail *Archisotoma beselsi* are very abundant on the rocks, and in the case of the springtail, on the surface of rock-pools.

When we pass to the inner parts of the fjords on the west coast, conditions become much more favourable, and a comparatively rich community of sea-

weeds develops in many places. This is, however, still dependent upon the absence of floating ice, so that the rocks are usually bare of life in the neighbourhood of glaciers, unless they happen to be sheltered in some accidental way, as at Klaas Billen Bay, where a line of boulders keeps out the ice from one bay. Here the animals and plants grow chiefly on the sheltered sides of the boulders. The animal community on rocks in the fjords has been described in our other paper (29, pp. 250, 265). It may include hydroids, polyzoa, crustacea, halacarid mites, and molluscs, land-mites and springtails. Wading birds such as Sandpipers and Turnstones feed here. This fjord flora and fauna, just as in the case of the land animals and plants (see p. 256), foreshadow the development of the type found a little farther south, in the north of Norway. Molluscs such as the Mussel, *Mytilus edulis*, and the Periwinkle, *Littorina littorea*, do not now occur in Spitsbergen, although they are found in comparatively recent Quaternary deposits, which indicate the change that a slight improvement of the present climate would produce.

(b) Shingle shores.

These differ from the last in being much poorer in sea-weeds (Pl. XXIX, Phot. 11). In Liefde Bay more or less stunted examples of *Fucus evanescens* occur, but the plants are never as well developed as on the rocks. The marine animal life is correspondingly poorer, consisting chiefly of *Gammarus locusta*. The stones afford cover for various mites, springtails and worms, which may be quite numerous in places. On the south shore of Reindeer Peninsula the following were found:

| | |
|---------------------------|--|
| MITES (Acarina): | <i>Bdella littoralis</i> <i>Chromotydeus arcticus</i> |
| SPRINGTAILS (Collembola): | <i>Archisotoma beselsi</i> <i>Achorutes viaticus</i> <i>A. longispinus</i> <i>A. minute red sminthurine</i> |
| WORM (Oligochaeta): | <i>Lumbricillus aegialites</i> |

The shingle fauna of the inner fjords was not worked out completely by us, but seems to have a similar invertebrate fauna.

(c) Muddy shores.

These, where sheltered, develop salt-marshes of various kinds, except in the barren regions of Hinlopen Strait, where they are devoid of life. The salt-marshes are usually formed of mosses, and frequently are found inside the little lagoons which are so common all round the coasts of Spitsbergen. At Lomme Bay the mud was covered with *Bryum teres* and *Catabrosa algida*; in Liefde Bay salt-marshes of *Bryum* sp. and *Catabrosa algida* occur; while in Klaas Billen Bay, there is a community of *Bryum nitidulum* and *Glyceria vilfoidea*. There is a distinctive animal community living in the mosses, but

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this has only been studied at Liefde Bay and Klaas Billen Bay. At the former place the following were found in the moss:

| | |
|---------------------------|--|
| SPRINGTAILS (Collembola): | <i>Achorutes viaticus</i> <i>Folsomia 4-oculata</i> |
| WORMS (Oligochaeta): | <i>Enchytraeus albidus</i> * <i>E. aporus</i> * <i>E. liefdeensis</i> * <i>E. muscicola</i> |

The three species marked with an asterisk appear to be confined to this habitat.

At Klaas Billen Bay a similar community has been described by us (29, p. 259), the species being somewhat different (e.g. the common worm was *Enchytraeus crymodes*, while two additional species of Collembola were present, one of which, *Folsomia sex-oculata*, does not occur in Liefde Bay).

2. DRIFT-LINE.

The drift-line of these arctic shores is usually covered with drift-wood brought over from Siberia by the polar current, together with a good deal of *Laminaria* and other sea-weeds washed up by storms. Even on Nordenskiöld Island and Low Island there were piles of sea-weed on the shore in places. In winter this material gets pushed up a foot or more by the freezing of the sea, and so forms a rather definite zone quite above the normal influence of tides, though not above the reach of storm-waves. These conditions (dampness and ample food-supply) attract a number of animals, both from the intertidal zone, and from the land. A mixed assemblage is therefore formed, consisting of worms and springtails and mites from below, together with flies, mites, spiders, and springtails from the land. One or two animals occur only or almost only in this community, e.g. *Fucomyia frigida* and *parvula*, *Enchytraeus albidus* and *Scutovertex lineatus*. In the barren regions *Lumbricillus aegialites* is widely distributed at the drift-line, or above it. In these areas, *Bdella littoralis* which is a very common intertidal and drift-line mite, has entirely changed its habits, and occurs only on the fjaeldmark further inland (e.g. on Waigat Islands, Foster Islands, and Cape Eremit).

Passing to Liefde Bay, we find a great increase in the number of drift-line species. The following were found on the south side of Reindeer Peninsula, in various spots:

| | |
|---------------------|--|
| SPIDERS (Araneida): | 1 <i>Erigone psychrophila</i> 1 <i>Typhochrestus spetsbergensis</i> |
| MITES (Acarina): | 1 <i>Bdella groenlandica</i> 4 <i>B. littoralis</i> 1 <i>B. pallipes</i> 2 <i>Bryobia praetiosa</i> 4 <i>Chromotydeus arcticus</i> 2 <i>Rhagidia gelida</i> 3 <i>Scutovertex lineatus</i> 1 <i>Sphaerozetes notatus</i> |

| | |
|---------------------------|---|
| FLIES (Diptera): | 3 <i>Fucomyia frigida</i> 3 <i>F. parvula</i> |
| SPRINGTAILS (Collembola): | 1 <i>Achorutes longispinus</i> 1 <i>A. viaticus</i> 4 <i>Archisotoma beselsi</i> 2 <i>Onychiurus groenlandicus</i> |
| WORMS (Oligochaeta): | 3 <i>Enchytraeus albidus</i> 4 <i>E. liefdeensis</i> 4 <i>Lumbricillus aegialites</i> |

The numbers indicate the usual habitats of these animals (1 = fjaeldmark; 2 = damper fjaeldmark or grass-turf; 3 = drift-line; 4 = intertidal). From this the mixed nature of the community will be seen. The drift-line is usually fairly rich as regards the actual number of individuals, and is accordingly much frequented by Purple Sandpipers and Turnstones. We have very little data about the drift-line community in the inner fjords, but what we have indicates that it is similar to that given above; at Green Harbour the following were collected among sea-weed and other debris at the drift-line:

| | |
|---------------------------|--|
| MITES (Acarina): | <i>Sphaerozetes notatus</i> <i>Cyta brevirostris</i> |
| BEEBLE (Coleoptera): | <i>Atheta prope frigida</i> |
| SPRINGTAILS (Collembola): | <i>Achorutes viaticus</i> <i>A. longispinus</i> <i>Agrenia bidenticulata</i> <i>Archisotoma beselsi</i> |
| WORMS (Oligochaeta): | <i>Enchytraeus albidus</i> <i>Lumbricillus aegialites</i> |

The beetle, *Atheta*, and the mite, *Cyta brevirostris*, are indications of the more favourable climate of Green Harbour.

3. SCAVENGERS IN DEAD ANIMALS.

These are included in this section on maritime communities, since most of our data relates to the dead bodies of animals lying on or near the shore. There are not now very many mammals in Spitsbergen, so that scavengers are comparatively rare. However, the following cases were encountered:

1. Two dead arctic foxes on Deer Bay Island contained larvae, pupae, and emerging adults of the blow-fly *Phormia atriceps*; a small fly *Borborus fumipennis*, also belonging to a scavenging group, was found also under the body. Spiders (*Erigone arctica*) were running about.

2. A dead whale, which had been lying at Green Harbour for several years, just above the shore line, containing vast numbers of larvae, pupae and emerging adults of *Phormia groenlandica* (July 3rd to 5th, 1924). The blow-flies were encountered at distances of a mile or more from the whale, on July 5th; they made a loud humming noise as they flew, which may explain the story we were told of the existence of "bees" in Spitsbergen.

3. As noted in our other paper (29, p. 259), a dead ring-seal on the shore of Klaas Billen Bay contained vast numbers of worms (*Lumbricillus necrophagus*) together with a few *Henlea* and mites.

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4. It may be worth noting that large blue-bottle flies (*Calliphora erythrocephala*) were noticed flying on the deck of our expedition ship, while we were going down Wood Bay on August 21st, 1924. This illustrates the possibility of ships carrying new animals to Spitsbergen.

VIII. CLIMATIC ZONES.

1. The climate of Spitsbergen is greatly influenced by the Gulf Stream drift, which produces on the west coast a climate such as occurs elsewhere only at rather lower latitudes. The Gulf Stream drift passes northwards from Northern Scandinavia to the west of Bear Island but does not approach Spitsbergen at all closely until it gets near the region of Icefjord (about half way up the west coast). The greatest effect is, however, probably at the north-west corner, where the current sweeps round and then passes along the north coast. The proofs of this drift are many: perhaps the most interesting was the discovery by Torell in 1861 (23, p. 72) of a seed of *Entada scandens*, a tropical plant from Central and South America, at Shoal Point in Murchison Bay. Green fishing floats were sometimes noticed in 1923 in Liefde Bay and Wijde Bay, while pieces of raw rubber, derived from ships sunk by submarines in the Atlantic during the War, were collected on the shore of Liefde Bay. The fishing floats must have been brought from Scandinavia, as also birch bark found in many of the northern fjords of Spitsbergen, and on North Cape. In opposition to the warmth-bringing Gulf Stream drift is the Polar current, which sweeps down the east and south coasts of North-East Land. This current then divides, part of it passing up Hinlopen Strait, while the main portion goes further south past Edge Island and Barents Land, to South Cape, and on to Bear Island. The Polar current brings with it drift- or pack-ice (and quantities of drift-wood from Siberia) which may sometimes completely envelope parts of the coast during the summer. The ice-pack exerts a profound influence on the temperature of the shores adjacent to it, the parts of the archipelago where it frequently occurs experiencing a much colder climate.

Fogs are frequent in these regions, especially where the Polar current meets the warm drift from the south-west (as at South Cape and Bear Island, and in Hinlopen Strait). On the north coast of North-East Land the effect of the Gulf Stream is greater and sea-ice rarely comes west of North Cape in the summer, there being an ice-free zone of varying width between the north coast of Spitsbergen and the Polar ice-pack. In Hinlopen Strait, ice carried northwards is usually stopped by the Foster Islands, which have been termed by mariners "the key to Hinlopen Strait." The northern part of the strait thus tends to keep relatively clear of ice in summer. As a result of these two currents, the warm and the cold, a gradient in climate can be traced as one passes from the north and east, to the south and west.

2. As mentioned previously, North-East Land is least subject to the warming effect of the Gulf Stream, and consequently a large ice-dome occupies the centre of the island. A similar ice-cap is present in New Friesland on the opposite side of Hinlopen Strait. Around the coast ice-free areas are left, these having been abandoned by the retreating ice-cap—a process which is still in progress, but which is not at all regular, since there are minor cycles superimposed on the larger one. On these rocky areas frost-weathering is at its maximum, and so effective has this been that it is unusual to find a boulder of any soft rock there; only hard granite, gneiss, or dolerite, can resist the tremendous frost-splitting. Over this part of Spitsbergen the exposed land surface is covered everywhere with shattered rocks and stones, soil being very scarce. The vegetation (as described in Section III) is extremely sparse, consisting of scattered tufts of a few species, of which the Arctic Willow (*Salix polaris*), the Arctic Poppy (*Papaver radicatum*) and the Purple Saxifrage (*Saxifraga oppositifolia*) are the most important. The poppies indeed seem to thrive here better than in more favoured spots. Animal life on land is equally scarce, but the sea-birds are numerous. Around Hinlopen Strait the vegetation is slightly less meagre than it is further east, but its general character is the same, and the whole region may be classed as forming a single climatic zone—**Zone 1, or Barren Zone**. In the most favourable spots is found a fjaeldmark or open community in which *Salix polaris* and the rush *Luzula confusa* are the most prominent plants; but closed communities of higher plants practically never occur except around bird-cliffs. An interesting feature of the region is the almost complete absence of life in the intertidal areas, owing to the abrading action of floating ice. On the other hand, there is a special fauna on the ice-pack itself. The Barren Zone occupies nearly the whole of North-East Land and the shores of Hinlopen Strait described in Section III of this paper; the Witches Islands, from which *Dryas octopetala* is entirely absent (1); the eastern shores of Barents Land (Kukenthal (17) was able to find only six species of phanerogams at Cape Barth in 1889); probably the eastern shores of Edge Island; and Hope Island, which has been recently explored by Iversen and Kofoed (15).

Until the visit of the Cambridge Expedition to Storfjord in 1927, little was known about the flora and fauna of that region. Through the kindness of Mr A. P. G. Michelmores, who acted as botanist and entomologist on that expedition, we are enabled to indicate in a general way the relations of the vegetation to that of the rest of Spitsbergen, and thus to fill in on our map the largest remaining blank space. Mr Michelmores will be publishing his results in full later on, and we do not wish to anticipate them; but it can be stated that the shores of Edge Island, Barents Land and West Spitsbergen, which form Storfjord, fall in a general way into the *Dryas* Zone, in the composition of their flora, although *Dryas* itself was only found at Cape Lee, Mohn Bay, and Whales Bay. The occurrence of certain species locally (e.g. *Erio-*

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phorum scheuchzeri) may indicate a still better climate in some spots; but *Cassiope* was not seen at any place visited by the party. Mr Michelmores's final results should be of great interest in settling this and other points.

The district around South Cape certainly comes under the Barren Zone, as also does Bear Island, 120 miles (192 km.) further south—at least as far as the general vegetation is concerned. East of Spitsbergen, Franz Josef Land is a grim example of the most extreme type of this zone.

3. In West Spitsbergen, the exterior coastal regions enjoy a more favourable climate, in which more species of flowering plants can exist, and in these regions the most highly developed vegetation is a fjaeldmark or dwarf-shrub heath of *Dryas octopetala*, instead of the *Salix-Luzula confusa* fjaeldmark of the Barren Zone. This zone we therefore call **Zone 2**—the **Dryas Zone**. Frost-action, although still very severe, is not so dominating as in Zone 1, and soil is usually to be found, there being associated with it some very curious frost phenomena, which are of importance in the development of the vegetation. The "polygonal soils," which are the most important of these, have been described in the section on Reindeer Peninsula (p. 222), and also for Prince Charles Foreland (29, p. 242), while they have also been described by one of us in a separate paper (8). The maritime districts, however, suffer from the frequent sea-fogs and low clouds, which reduce the sunshine, at the same time increasing the relative humidity of the air. Clear weather is decidedly uncommon in this zone even in midsummer, and consequently the heat necessary for the ripening of the seed of the later-flowering species is not available.

As one passes up the many long and narrow fjords which intersect the interior of West Spitsbergen, a change in the climate gradually takes place. Sea-fogs do not penetrate far into the fjords, while low-lying clouds are often robbed of their moisture or are dispersed by the heat from the land near the entrance. As a result, clear weather is more frequent as one approaches the heads of these fjords, insolation is greater, and this again prevents further precipitation. Cases of non-penetration of fogs and clouds were observed several times at Liefde Bay; often, while Reindeer Peninsula was covered with a thick blanket of clouds, Wood Bay farther inland was bathed in sunshine. Another important result of this gradient up the fjords is its effect on snowfall. Early autumn snow which fell in Liefde Bay covered Reindeer Peninsula to sea-level; at Svensen Bay on the opposite coast, but farther in, there was no snow below 200 to 300 ft. (60 to 90 m.); at Jacobsen Bay the lower snow-line was 700 to 800 ft. (210 to 240 m.) while at Cape Auguste Victoria and Cape Roos, which are even farther in from the sea-coast, the snow lay only above 1000 ft. (300 m.). In the case of such snow which persists, the ripening and distribution of seed is either prevented or delayed until the spring, and this must exclude late-flowering plants (unless they ripen seed very rapidly) from the coastal districts of Zone 2. A factor which exerts an

important effect in producing the climatic gradient in the fjords is the prevalence of föhn winds down the glaciers. These winds, warmed by their descent from the high-pressure area inland, to the lower pressure at sea-level, impinge on the land near the heads of the fjords, (where the glaciers debouch), and warm it up; they then pass down the fjords, their effect naturally lessening as they proceed. Near the mouths of the fjords fogs are formed.

4. Corresponding to this gradient of climate in the fjords, is a gradient in the vegetation. It has long been recognised that nearly all the rarer species in Spitsbergen are concentrated in the interiors of the fjords, particularly in Icefjord; as far back as 1883 Nathorst (22) gave a map illustrating the fact that 95 per cent. of the flora was found within an area comprising the interiors of Icefjord, Wijde Bay, and Bell Sound, etc. It was pointed out that the rarer species were sub-arctic or perhaps boreal species which could only find suitable conditions for existence in the sunny interiors of the fjords. No one, however, seems to have mentioned that associated with this gradient in the number of species, there is a gradient in the plant communities as one passes up the fjords, although naturally one is a consequence of the other. Careful correlation of all available records with our own observations, shows that immediately the outer coastal fog-belt is left behind, heaths of the arctic white bell-heather, *Cassiope tetragona*, are found—provided edaphic and topographical conditions permit. Lundager (19) has noted the same restricted occurrence of *Cassiope* in eastern Greenland, and no doubt it is a general phenomenon in the Arctic. In Liefde Bay it was possible to trace the gradual appearance of *Cassiope* in the fjord. On Reindeer Peninsula at the mouth, and on the Station Islands and Canard Islands near by, no *Cassiope* was found (even on the big erratic blocks of gneiss which had been colonised by other plants). There was also none on the mountains at the base of the peninsula. All these areas are in the coastal fog region. At Mouette Islands, farther up the bay, a little *Cassiope* was noted; while at Cape Roos on the inner coast opposite Reindeer Peninsula the plant was more abundant, but not particularly luxuriant. At Cape Auguste Victoria still farther in, a considerable amount was seen; while, finally, at Bock Bay extensive and luxuriant heaths of *Cassiope* occur. At all the localities but the last, the rocks are of the same nature, namely, Devonian shales mixed with harder quartzites; but at Bock Bay schists predominate. The latter certainly provide a more suitable substratum for *Cassiope* than the shales; but even allowing for this, the increase from mouth to head of the fjord is very obvious. This zone is therefore termed by us the **Cassiope Zone**—**Zone 3**. Good examples of areas in this zone are Aldert Dirkses Bay, Danes Island, and Amsterdam Island, and the interior of Lomme Bay. The two islands mentioned form an exception to the fjord distribution of *Cassiope*, this being due probably to the close vicinity of the Gulf Stream drift to that corner of Spitsbergen, and to the favourable conditions provided by the granitic rocks of which the islands are composed. Smeerenberg Sound, lying

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between Danes and Amsterdam Islands and the mainland, was in old times the centre of the Dutch whaling industry, because it was nearly always ice-free during the winter; this indicates sufficiently the favourable climate here.

In the bog areas *Eriophorum scheuchzeri* comes in at the same point as *Cassiope* on the dry areas, and acts as a second indicator of the climatic gradient.

5. With further penetration into the interior, especially in the three longer fjords, *Cassiope* maintains itself but is accompanied by a more varied flora, which does not occur elsewhere in Spitsbergen. This richer flora seems to be most strongly developed at Coles Bay and Advent Bay in Icefjord, together with Sassen Bay; and here *Betula nana* finds its only stations. The inner fjord flora is perhaps best characterised by *Empetrum nigrum*, which, judging from its occurrence in other arctic countries, would form heaths in Spitsbergen if the climate were slightly better. At present it nowhere forms communities of any extent. In this region, it is worth noting, are the only cases of peat formation in the absence of manuring by birds. Even here it reaches no great development, *Sphagna* being uncommon. The presence, however, in the interior of the fjords of such plants as *Betula nana*, *Rubus chamaemorus*, *Eriophorum angustifolium* (forma), *Vaccinium uliginosum*, together with the *Sphagna*, indicates that a relatively slight amelioration of climate would produce moors (tundra) of the typical sub-arctic type. This interior zone we term the **Inner Fjord Zone (Zone 4)**.

The areas occupied by the various zones are shown in the accompanying map, but it should be remembered that in most parts of the country only a narrow strip of land supports the vegetation proper to any particular zone; as one passes inland and ascends the mountains the vegetation becomes sparser, and eventually permanent névé or highland ice is reached. Although the large fjords exhibit the vegetation gradient most effectively, such a gradient occurs in all the fjords. For instance, all the fjords on the north-west coast of North-East Land, although being in Zone 1 at their mouths, yet have *Dryas* in their interiors and these are therefore quite definitely in Zone 2. Consequently there are often isolated patches of the more favourable climatic areas surrounded on all sides by more barren districts.

6. As has been indicated in previous sections of this paper, the sequence of plant communities as one passes from Zone 1 to Zone 4, can be studied on several of the important rock types, particularly the gneiss-granite-schist series and the shale-sandstone series. The dolerite series also shows a similar sequence of vegetation, but we were unable to examine a complete gradation of types, especially for Zones 3 and 4, where dolerite is not particularly common. We will therefore confine our observations to the other two rock-series. The first thing that strikes one on examination of the vegetation-sequence on these rocks, is that although in general features they resemble one another, yet there are certain distinctions between them. In the most

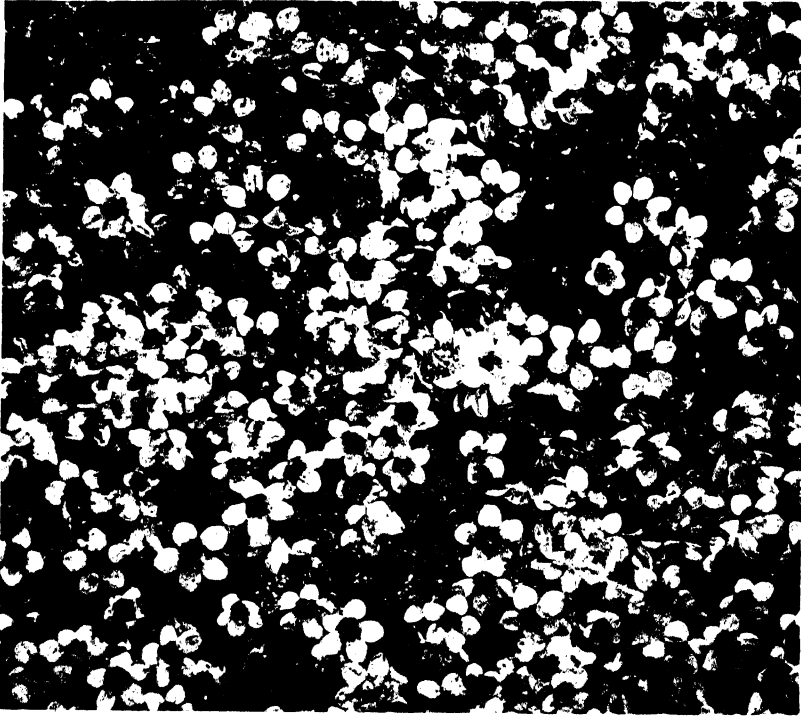
severe part of Zone 1 there is little to choose between the two sequences since the conditions limit the amount of variation possible; but on the granite-gneiss areas in the more favourable regions in this zone, *Racomitrium* heaths are characteristically developed. These may also be present on the sandstone areas, as at Bear Island, but are often quite lacking. In the other zones the improvement in the climate tends to favour the production of heaths, and these undoubtedly develop more rapidly and more luxuriantly on the granite-gneiss areas than on the shale-sandstone. This is illustrated by the highly developed *Cassiope* heath on granite at Aldert Dirkses Bay, whereas similar luxuriance is never reached on sandstone in the interior of Liefde Bay, although further from the coast. Also in Icefjord the very luxuriant *Cassiope* heath on schist at the De Geer Range in Klaas Billen Bay, contrasts with the rather sparse heaths at Advent Bay, Cape Boheman, and other places on sandstones. Similarly, *Empetrum* is found at Aldert Dirkses Bay, whereas even in the interior of Icefjord it only occurs locally on sandstone. It is interesting to note that neither *Cassiope* nor *Empetrum* is well developed in limestone areas, even in the most favourable parts of Icefjord; here, obviously, the soil is even more inimical to heath formation. All these points go to show that soil conditions may considerably modify some of the details of the vegetation sequence along the zones of climate, although this preserves a general similarity on all soils. No doubt a careful examination of the cryptogamic floras of the different rock-series would show significant differences, especially among the mosses; indeed, Berggren (1 b) pointed out many years ago the numerous species of mosses restricted to one or more of the rock-groups, but he did not study the subject from the point of view taken here. The modification of the usual climatic effects by soils has been noted before by Resvoll-Holmsen (25 a), but it seems to be less marked than in more temperate countries.

7. The most striking exceptions to the above statement are the nitrophilous communities, which have already been dealt with rather fully. Here the great improvement in the edaphic conditions allows of the maintenance of communities much more luxuriant than those on the unmanured ground around; and these communities remain more or less unchanged, as regards dominant plants, throughout all four climatic zones. As the nitrophilous effect is usually associated with steeply inclined slopes, the two factors together tend to neutralise the effect of climate, but this only applies to certain species. It must be remembered that the gradient Fjaeldmark—*Dryas*—*Cassiope*—Inner Fjord Flora is not influenced by manuring, since neither *Dryas* nor *Cassiope* is favoured by it. In fact a new series of grass-herb communities of a more sub-arctic type is established, instead of the arctic fjaeldmark and heaths.

8. The distribution of *Dryas* in Spitsbergen in relation to soil and underlying rock is of great interest. In Northern Sweden (Torne Lappmark) Fries (12) gives it as a marked calcicolous species, while other writers have

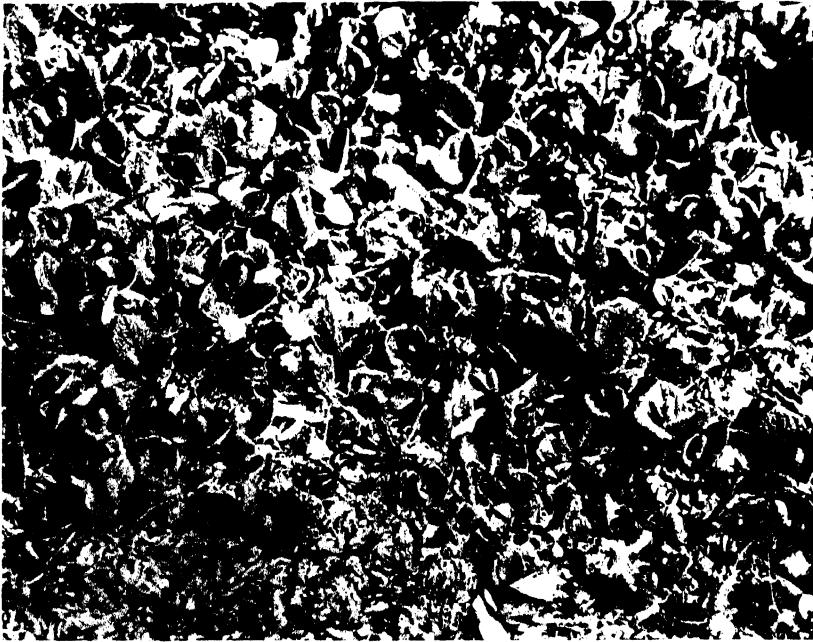
mentioned a preference for, or even restriction to, calcareous soils in the Alps, Carpathians, Caucasus, etc. Schröter (27) mentions that *Dryas* is reported to be indifferent in the Western Alps, but sums up by saying that the species prefers calcareous soils. It is significant however that in cases in which it occurs on assumed non-calcareous soils, no one has as yet carried out any detailed examination of the soils or habitat in question. Marret (20), indeed, states that *Dryas* is restricted to calcareous soils and that superficial observation is responsible for contrary reports. He quotes Beauverd as stating that the distribution of *Dryas* on crystalline rocks is a precise indicator of the presence of lime locally.

In Spitsbergen, on the other hand, *Dryas* seems to grow equally well on all types of soil, and it is important to note that on Reindeer Peninsula and Prince Charles Foreland, where it is at the extreme limits of its range climatically, it occurs on sandstones and quartzites which are very poor or lacking in lime. An examination of the records of occurrence of *Dryas* which we have available seems to indicate that *Dryas* is indifferent to the presence of calcium as such in the soil, but that it cannot tolerate an acid reaction. It is an easily observed fact that as the polar regions are left, peat formation becomes more and more abundant on soils devoid of some neutralising agent, with the result that heath plants which prefer an acid soil reaction occupy an increasingly greater proportion of the ground. Naturally a high precipitation tends to hasten peat formation on acid rocks and to leach out soluble salts from slightly basic ones, so that peat can be formed. In Spitsbergen there are two factors which act against peat formation except in the wettest places; the unfavourable climate in general, which prevents luxuriant growth and maintains open communities in most places, and secondly, the small precipitation, which may be only 15 in. (35 cm.) or less per annum. Although the snow-water saturates the ground everywhere for a few weeks in the early summer, the effect of this soon wears off and after that most of the higher ground becomes dry. Consequently, the small deposition of plant litter is easily disposed of by putrefactive organisms (in spite of the rarity of the latter), by scavenging animals, by wind, and no doubt in places by the snow-water itself at the annual thaw. This must result in a neutral or very slightly acid soil-water even on non-calcareous rocks, which enables *Dryas* to grow. It is significant in this connection that on such rocks *Dryas* only forms communities on the drier tops of small hills or mounds, or on well-drained slopes; whereas, on the other hand, it is found on the quite flat raised beaches, in valleys, and in other rather damper places in limestone areas (e.g. Gips Valley and Klaas Billen Bay, see 29, pp. 261, 275). In such places, in spite of the vegetable debris accumulated by mosses, the telluric water is probably alkaline and prevents formation of humic acids. As mentioned previously, it is now very doubtful if any of the *Dryas* communities in Spitsbergen come into the category of heaths (as was assumed previously by us, cf. 29, pp. 260, 261, 282); and indeed it is doubtful if *Dryas*



Phot. C. S. Elton

Phot. 22. The purple saxifrage (*Saxifraga oppositifolia*), on Deer Bay Island (at the head of King's Bay), July, 1924. This species is a common dominant on unfavourable soils, and is visited by a number of small flies, especially of the genus *Camptocladius*.



Phot. C. S. Elton

Phot. 23. *Salix reticulata*, forming a closed carpet, on Deer Bay Island (at the head of King's Bay). Among the *Salix* were numbers of weevils (*Tachyerges saliceti*) together with a comparatively rich community of other animals. Leaves of *Dryas* can also be seen near the bottom of the photograph.

"heaths" occur elsewhere either. Fries (12, p. 74), when dealing with Northern Sweden, mentions under his "Heide Series" a "Flechten-reichen *Dryas octopetala* Assoziation," but states that it is especially developed on dolomite! He also says, in describing an example, that humus was absent. The presence of true heath plants, such as *Cassiope tetragona*, *Empetrum*, etc., does not prove that the soil reaction is other than neutral. Mossy *Dryas* associations also occur in Scandinavia on calcareous soils at high altitudes, and here humus may occur. However, the floristic composition of these communities is even less indicative of acid conditions than that of the "heaths." It seems therefore necessary to carry out a series of pH and lime-requirement determinations in *Dryas* communities in the Arctic and elsewhere in order to clear up this point properly.

9. There is a further aspect of the climatic zonation which requires consideration: an examination of the distribution charts of the various species shows that a number do not conform to the climatic zonation shown on the map. For instance, *Campanula uniflora*, *Cystopteris fragilis*, *Salix reticulata* (Pl. XXXV, Phot. 23), *Lycopodium selago*, *Ranunculus pallasii*, and *Saxifraga aizoides*, although otherwise confined to the interior of the fjords, occur on some relatively sunless localities on the west coast, e.g. west coast of Prince Charles Foreland, or the Dun Islands near Horn Sound. The fact that the distribution maps of such species show similar peculiarities seems sufficient evidence that the latter are not due merely to accidents of dispersal. A possible explanation is that the higher air temperature along the west coast, due to the proximity of the Gulf Stream drift, compensates, in the case of certain species, for the absence of sunshine. The study of the flora of Bear Island supports this idea, for although the very meagre character of the vegetation, and certain features of the climate (fog and exposure), place it in Zone 1, yet the presence of such phanerogams as *Salix herbacea*, *Rhododendron lapponicum*, *Salix reticulata*, and *Sedum rhodiola*, suggests a more favourable climate. (A number of sub-arctic mosses have also been recorded from Bear Island and do not occur in Spitsbergen.) This idea is borne out by temperature records which show that the mean annual temperature of Bear Island is several degrees higher than that of West Spitsbergen, and the suggestion receives strong additional support from the composition of the fauna (see below).

10. An analysis of the flowering plants of the different zones was made according to the system of "life-forms" elaborated by Raunkiaer (25), and "plant spectra" of the zones have been obtained. These are given below, together with those of Hope Island (which may be considered as an extreme example of Zone 1), and Bear Island, which lies considerably south of Spitsbergen, but belongs to it floristically.

The gradual increase in the number of species as one passes from Zone 1 to Zone 4 is notable, while the spectra themselves are interesting. As is the usual case in these latitudes, the chamaephyte group is especially characteristic,

and it will be seen that there are over 20 per cent. of chamaephytes in each of the areas given above. The hemicryptophytes, although predominating in actual numbers, are not so important as a climatic index, since they may be almost equally abundant much farther south at low levels, e.g. in Scotland.

| District | Number of species | Percentage of each life-form present | | | | | | | | | |
|----------|-------------------|--------------------------------------|---|----|---|-----|------|----|----|-----|-----|
| | | S | E | MM | M | N | Ch | H | G | HH | Th |
| Hope I. | 20 | — | — | — | — | — | 25 | 70 | 5 | — | — |
| Zone 1 | 38 | — | — | — | — | — | 26 | 66 | 3 | 5 | — |
| Zone 2 | 69 | — | — | — | — | — | 34 | 56 | 6 | 4 | — |
| Zone 3 | 91 | — | — | — | — | — | 27 | 60 | 10 | 2 | 1 |
| Zone 4 | 127 | — | — | — | — | 1.5 | 21 | 58 | 15 | 3 | 1.5 |
| Bear I. | 53 | — | — | — | — | 2 | 26.5 | 53 | 11 | 5.5 | 2 |

An examination of the chamaephyte percentages shows that, contrary to expectation from Raunkiaer's figures the chamaephyte percentage does not increase steadily from Zone 1 to Zone 4, but has a maximum, which may or may not be significant in Zone 2.

A comparison of the Bear Island figures with those for the various climatic zones of Spitsbergen shows in an interesting way that, although the island lacks both *Dryas* and *Cassiope*, and is subject to many of the climatic conditions characteristic of Zone 1, the spectrum is on the whole similar to those of Zones 3 and 4 in Spitsbergen—thus confirming the suggestion made above, that the climate of Bear Island is not so bad as it seems.

11. The animals of Spitsbergen have not been collected sufficiently extensively in an ecological manner to allow us to draw more than very broad conclusions about the zonation of the communities. But they do quite definitely follow the general zonation of the plants, both along the main line from east to the west, and also up the fjords. This gradation is, however, complicated in southern and south-western Spitsbergen by the gradient in air-temperature which (as explained in part 9 of this section) also produces exceptions among the plants. Only this air-temperature gradient interferes much more with the animals than with the plants, so that a number of species of animals occur only in the inner parts of fjords on the north and west, but near or on the coast in the south. This is what we should expect in view of the greater dependence of animals upon temperature than upon light. We shall return to this point later.

12. In the North-East Land region, only 9 species of land-animals were found, these forming a sort of skeleton food-cycle, which is unable to maintain itself without obtaining food from other communities. In the *Dryas* Zone there are far more species, e.g. about 30 on Reindeer Peninsula, and about 25 on the part of Prince Charles Foreland examined. These animals consist of spiders, mites, springtails, flies, a very few parasitic hymenoptera, and one worm, together with a few birds. The spider *Erigone psychrophila* is common all over Reindeer Peninsula, occurring also in Lomme Bay (*Dryas* or *Cassiope*

Zones), but not in the barren areas. Passing to the *Cassiope* Zone, we find a similar community, varying much locally, but containing several animals not found in less favourable places, e.g. the flies *Acroptera frontata*, *Trichocera lutea*, and the spider *Erigone arctica*. When we reach the most favourable parts of the inner fjords, a number of new forms appear, which foreshadow (just as in the case of the plants) the richer fauna of sub-arctic regions. There is an aphid (*Aphis* sp.), preyed upon by a hover-fly (*Syrphus tarsatus*) which is probably parasitised by a braconid (*Bassus arcticus*); a beetle (*Tachyerges saliceti*) at the head of King's Bay and at Coles Bay; a sawfly (*Pristiphora frigida*) found, among other places, at Advent Bay and Green Harbour and Bell Sound; several flies appear, such as *Rhamphomyia caudata*, *Exechia frigida*, and a mosquito (*Aedes alpinus*). Various spiders have only been found in a few localities in the inner fjords, e.g. *Micaria eltonii* on the De Geer Range in Klaas Billen Bay, and *Erigone tirolensis* on the mountains above Cape Thordsen in Icefjord.

13. The examples given above are sufficient to show the type of gradation found among the animal communities; but much further work will have to be done, especially in the inner fjords, before exact tables of comparison can be drawn up. Apart from the work of our own expeditions, the only intensive work on the insects is that done by Holmgren and published in 1869 (13). It is to his fine work that we owe most of our information about the fjord insects.

We have pointed out above that some animals disagree with the general series of life-zones found in Spitsbergen. These exceptions may be considered under two heads: those in south and west Spitsbergen, and those on Bear Island. To take the first group: examples are the occurrence of a sawfly (*Pristiphora frigida*) in Horn Sound and at Whale's Point on the south of Edge Island; the occurrence of *Micryphantès nigripes* (otherwise only found at Cape Thordsen) in Horn Sound; and the existence of certain fjord animals on Prince Charles Foreland (where *Cassiope* is entirely absent), e.g. *Cyta brevirostris*.

14. The fauna of Bear Island illustrates the point particularly well. There are at least 31 species of animals on the fjaeldmark, compared with 9 in North-East Land. Among these are some forms found only in the fjords in Spitsbergen: the spider *Coryphaeus holmgrenii*, and the sawfly *Pristiphora frigida*. In addition, there are several southern species not found in Spitsbergen at all: the Golden Plover (*Charadrius apricarius*); two sawflies (*Pontania birulae* and *Amauronematus villosus*); and a springtail (*Onychiurus neglectus*). Among the birds, the Greater Black-backed Gull (*Larus marinus*), the Common Guillemot (*Uria troille*), the Norwegian Puffin (*Fratercula arctica*), and the Common Scoter (*Oedemia nigra*) also indicate the link with Norway; while two fresh-water copepods (*Cyclops gigas* and *C. vicinus*) and a fresh-water worm (*Nais josinae*) also occur to the south but not in Spitsbergen. And yet

the vegetation of Bear Island resembles in its general features that of Hinlopen Strait.

15. There is one more feature of the animal zonation which demands notice. Certain species appear to change their habits quite definitely as we pass from one climate to another. For instance, *Bdella littoralis* is a land-animal in Zone 1, and strictly a maritime animal in Zones 2 to 4. The worm *Enchytraeus albidus* is a drift-line animal in Spitsbergen, but occurs on the fjaeldmark on Bear Island. *Erigone psychrophila* occurs as the common fjaeldmark spider in Zone 2 (on Reindeer Peninsula), but is confined to the drift-line in most places in Icefjord. Finally, the bog springtails of the genus *Achorutes* become more and more important in the fjaeldmark, as we pass from Zone 4 to Zone 1.

These peculiar changes are correlated in most cases with the presence or absence of some other species. Thus *Bdella littoralis* occurs on the land chiefly where other species of *Bdella* are absent. *Enchytraeus* only comes on the fjaeldmark on an island from which *Henlea brucei* (the usual species) is absent. *Erigone psychrophila* only invades the land when *Erigone arctica* is not present: at Green Harbour and Klaas Billen Bay, *E. psychrophila* lives near the shore, and *E. arctica* on the fjaeldmark. The increase in abundance of *Achorutes* in the fjaeldmark is accompanied by a decrease in the numbers of *Isotoma viridis*, which is a very common fjaeldmark springtail in the fjords, but very scarce in places like Reindeer Peninsula, and absent from North-East Land. It does therefore look as if the habitats of these species were to some extent determined by the presence of closely allied species, or by species occupying the same ecological status or niche, and that by some obscure process which we call "competition" (not knowing what it really means) the one can oust the other under favourable conditions. In several cases the species were found living together (as *Bdella decipiens* and *B. littoralis* at Cape Eremitte and *Erigone arctica* and *psychrophila* on the shore at Klaas Billen Bay). These cases may either indicate that our suggestion of competition is not true, or more likely, that we see the process actually at work in such cases. In any case, the phenomenon seems an interesting one and deserves further attention.

IX. RELATION OF THE VEGETATION AND FAUNA TO THOSE OF OTHER COUNTRIES.

(a) VEGETATION.

The most obvious feature of the vegetation of Spitsbergen is its very high-arctic character. The archipelago lies not only entirely beyond the tree-limit, but also beyond the scrub-limit. None of the "grey willows" (e.g. *Salix glauca*, *S. lanata*) is found in Spitsbergen, so that the willow-brush so characteristic of Northern Scandinavia and Southern Greenland (and also

found in sheltered parts of Greenland as far north as lat. 69°) does not occur. *Betula nana* is very rare in Spitsbergen, and where it does come the communities dominated by it are very small in extent. Owing to this absence of the forest and willow zones, the highest form of vegetation is some type of dwarf-shrub heath, although even this is very poor in species. *Vaccinium uliginosum* has been found in one locality, but the common sub-arctic heath-forming shrubs, *Diapensia lapponica*, *Loiseleuria procumbens*, *Phyllodoce coerulea*, *Ledum palustre*, and *Rhododendron lapponicum*, are entirely absent. The only important heath-forming plant is *Cassiope tetragona*, since *Dryas octopetala*, although also a dwarf-shrub, more frequently occurs in fjældmark and in communities which perhaps may more accurately be termed "Wiesen." since superficial peat is often not produced. Unfortunately there are no pH records available from Spitsbergen, so that this point as yet remains a little doubtful. As already mentioned, *Empetrum nigrum* occurs locally, but never forms heaths of its own; the climate does not normally allow of ripening of the berries, although this does take place in favourable summers. From all the evidence it seems very probable that a slight improvement in the climate would allow *Empetrum* to form heath communities in the interiors of the fjords, and there it might be accompanied by *Vaccinium uliginosum*, *Betula nana*, etc. It may be noted that a similar relation between *Cassiope* and *Empetrum* seems to exist in the "Barren grounds" of sub-arctic Canada, where *Empetrum* fails to set seed at the northern edge of its range, and is replaced gradually by *Cassiope tetragona* (30). The general vegetation of Spitsbergen on dry ground is therefore similar to that of the upper "Regio Alpina" of Fries (11) in Northern Scandinavia. On the higher mountains of that country there are fjældmark communities with *Salix polaris*, *S. herbacea*, *Silene acaulis*, *Saxifraga* spp., and these agree closely in floristic composition with the general dry fjældmark in Spitsbergen. It is interesting to note that the two plants usually dominant on ground continually damp from snow-water in Scandinavia, namely, *Salix herbacea* and *Cassiope hypnoides*, are extremely rare in Spitsbergen and their places seem to be taken by mosses, the usual *Gymnomitria* not, however, being so prominent. This difference may be due to the smaller snow-fall of Spitsbergen, which results in the disappearance of snow-drifts before the end of the summer; but the snow-patch flora requires more careful examination.

"Wiesen" communities, occurring on fresh, well-drained soils, are frequently found in the more favourable parts of the archipelago, especially on slopes with a south aspect, and they compare fairly closely with those of other countries. Many of the rare plants of Spitsbergen occur in these places, particularly in the interiors of the fjords. The screes below bird-cliffs are often occupied by communities of this type, especially when facing south, and the large amount of grass (mainly species of *Poa*) is their most characteristic feature. Tall-herb communities, such as are dominated in Scandinavia by

Geranium sylvaticum, *Trollius europaeus*, *Archangelica*, etc., are, however, quite absent from Spitsbergen, and this fact again demonstrates the completely high-arctic nature of the archipelago. A similar difference is shown by North and South Greenland, and the presence of tall herb "Wiesen" or "meadows" seems to be correlated climatically with that of willow-scrub.

Coming to the wetter types of vegetation, the bogs, the difference between Northern Europe and Spitsbergen is more marked. Tundra, defined as swamp or moorland developed on more or less deep peat, is quite absent from the latter; indeed, peat formation is only found there on a very limited scale. The *Sphagna*, which are the chief mosses concerned in such tundras in Scandinavia, are quite local in Spitsbergen, and, even when they are present, do not dominate markedly in the bogs. In this respect the bogs agree with those of arctic Greenland (14, p. 99; 5), although in South Greenland *Sphagnum* bogs are found. The Spitsbergen bogs are dominated by species of *Hypnum*, *Brachythecium*, *Aulacomnium*, *Dicranum*, together with many other species of less importance, and the floristic composition is extremely variable. Kihlman (16, p. 8) mentions that in rare cases species of *Dicranum* form fairly thick peat in the Kola Peninsula, while *Webera nutans* may form peat 2 to 3 ft. (0.6–0.9 m.) thick in Greenland, so that *Sphagna* are clearly by no means necessary for the production of thick peat in the tundra. The fact is that in Spitsbergen conditions are not favourable for peat formation at all, for any mosses; this is because the precipitation over most parts of the country is not sufficient to keep up a constant supply of drainage water, apart from the melting of the snow, and many of the moss-bogs consequently dry up to a large extent in late summer. There are very few places where the water level in the soil remains the same for as long as a month; the soil is always drying up, as the snow-drifts gradually disappear, while the summer rainfall is almost negligible, and very irregular. These circumstances discourage the successful establishment of *Sphagna*, etc., which require a more or less continuous wetting for their best development. The vertical growth of mosses generally must be very slow in the Arctic, and during the summer period of drought, putrefactive bacteria, in spite of their relatively small numbers, can probably prevent any accumulation of humus. In addition, no preservative humic acids enter the bogs in the drainage water, owing to the lack of dry peat in the higher ground around. High moor, in almost all its forms, may therefore be said to be absent. Types of low moor, however, with perhaps alkaline telluric water, are frequent, the main species being *Arctophila fulva*, *Alopecurus alpinus*, *Eriophorum scheuchzeri*, *E. angustifolium* var. *triste*, *Juncus biglumis*, *Dupontia fisheri*, together with various other species. These communities are very similar to the ones occurring in Northern Sweden. The mosses are *Polytrichum strictum*, *Dicranum* spp., *Hypnum* spp., and others, but not *Sphagna*. Communities of large *Carices* are not found, this being a sharp distinction between the two regions; but smaller *Carices* occur locally.

One of the most striking features of the vegetation of Spitsbergen is the complete absence of true water-plants, owing to freezing of the water in winter to a depth of several feet, i.e. usually to the bottom. In Greenland a number of water-plants occur, but only in the central and southern parts.

On the whole, therefore, the communities of Spitsbergen fall into the same series as those of Scandinavia beyond or above the tree limit, but are more poorly developed, both from the point of view of luxuriance and of richness in species. Whole series of communities of a more southern type (woodland, scrub, and high moor) are absent, and the vegetation is on the whole similar to that of Scandinavia on the higher mountains and in the extreme north-east. In addition, since almost all the species occurring in Spitsbergen are also found in Scandinavia, the actual floristic composition of the communities agrees in a striking manner. With regard to Northern Greenland, the similarity in physiognomy is naturally very great, but the number of American species in Greenland, makes the floristic composition of the communities somewhat different; the resemblance becomes greater, the farther north we go in Greenland. The two countries really show an almost identically similar zonation of vegetation, the zones in Spitsbergen being compressed into a narrower belt. Southern Greenland has a vegetation intermediate between that of Spitsbergen and North Greenland on the one hand, and of Scandinavia and northern Canada on the other, and it enables us to get an idea of the probable development of vegetation in Spitsbergen in the event of an improvement in the climate—a change also foreshadowed by the interior fjord flora of Spitsbergen.

From the limited information which we have been able to collect, it appears that the zones of Spitsbergen—Fjaeldmark, *Dryas*, *Cassiope*, *Empetrum*, can also be traced in a broad way right across arctic North America, the first-mentioned zone being almost entirely confined to the arctic archipelago of Canada. The "Barren grounds" of the mainland of Canada fall partly into the *Cassiope* zone (in the north) but very largely into the sub-arctic zone, in which *Empetrum* and other dwarf-shrubs flourish.

(b) THE FAUNA.

Spitsbergen was almost certainly wiped quite clean of animal life during the last glacial maximum, and subsequent colonisation took place after the country had become separated from Europe by the Barents Sea; from Greenland it is separated by a deep trough. The fauna therefore consists of those species which have been able to make their way by some means or other across several hundred miles of arctic ocean in summer, or of frozen sea-ice in winter. The Reindeer seems to have come over the ice, while most of the insects have probably been carried or blown over during the summer. A remarkable case of long-distance dispersal has been described by one of us

in another paper, in which will be found a general discussion of the means of dispersal of the various invertebrates (6): in the summer of 1924, vast swarms of hover flies (*Syrphus ribesii*) and spruce aphids (*Dilachnus piceae*) were blown from Northern Europe on to the ice-cap of North-East Land—a distance of over 800 miles. They were alive when they arrived, but perished later in a blizzard; in any case they could scarcely have survived very long. A similar swarm of aphids was encountered by Parry off the west of North-East Land in 1827 (24, p. 201). It is to be supposed that the other insects reached the archipelago by similar means, or by transport on birds. The result of the isolated position of Spitsbergen is that many groups of animals are absent, although these are found in Greenland under similar conditions of climate and vegetation. Examples are various butterflies, also bumble-bees and tipulid flies.

Furthermore, several mammals are absent, e.g. the Lemming, Arctic Hare, and Musk Ox. The absence of Lemmings is reflected in the almost complete absence of Snowy Owls, and the fact that there are no Ermine (which eat the Lemmings); nor are there any Arctic Wolves (which eat Hares). Since the wolves also attack deer, it is probable that their absence is due rather to dispersal difficulties than merely to absence of food. These questions, in so far as they affect the mammals, will be treated in a separate paper.

The fauna of Spitsbergen differs therefore from that of similar places in the same zones of climate and vegetation, in being rather more impoverished. We have already (Section VIII) traced the gradual increase in complication of the food-cycle as the climate improves, and have shown how the most highly developed animal communities in Spitsbergen foreshadow in a general way the very complicated communities of sub-arctic and temperate regions. At the present time we know very little about the animals of the sub-arctic zone (*Empetrum*, etc.) and it is to be hoped that future work in some place like South Greenland or Lapland will bridge the gap between our knowledge of the food-cycles of high arctic countries and those of our own regions.

X. SUMMARY.

1. In 1923 we published in this *Journal* an account (almost entirely descriptive) of the animal and plant communities of certain parts of Spitsbergen and Bear Island. Further investigations in Spitsbergen have enabled us to co-ordinate these and our later observations into a general scheme, which makes it possible to explain the general distribution of the plant and animal communities in terms of four master factors: climate (insolation and air-temperature), soil, manuring by sea-birds, and water-supply.

2. The climatic gradient produced by the meeting of the Polar ice-pack with the Gulf Stream, brings about a corresponding gradient in the types of vegetation. This gradient can be divided naturally into four zones, (1) Barren

Zone, (2) *Dryas* Zone, (3) *Cassiope* Zone, and (4) the Inner Fjord or *Empetrum* Zone.

3. This gradient in plant communities has also been traced in the communities of land-animals, and in the intertidal fauna. By combining all these lines of evidence, we have constructed a provisional map showing the main life-zones for the whole of the Spitsbergen archipelago.

4. These zones can be traced on a much broader scale right across Greenland and Arctic Canada, and in the mountains of northern Scandinavia; and they demonstrate the very high-arctic character of Spitsbergen communities.

5. The gradient outlined above is interfered with by bird-manuring, which produces distinctive (and usually grassy) communities even in the most barren parts of Spitsbergen. The effects of bird-manuring on animals and plants were studied intensively in several cases.

6. It is impossible in a short space to summarise any of the other points dealt with, and the reader may be referred to Sections VIII and IX, and to the map, since these are to some extent summaries of the rest of this paper.

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For a more complete list of works dealing with the flora and fauna of Spitsbergen, the reader is referred to our previous paper (29).

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ECOLOGICAL NOTES ON THE BRYOPHYTES OF MIDDLESEX

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INTRODUCTION.

THOUGH there are several ecological studies of the bryophytes of particular English formations and associations, none dealing with all the moss-communities in a limited English district, comparable to Loeske's "*Die Moosvereine im Gebiete der Flora von Berlin*" (8), have so far been published. Such studies are useful in providing material for comparing the moss-vegetation of different habitats and so testing the diagnostic value of the bryophyta in ecology. Though Middlesex, from its small size and lack of variety, is not specially suitable for such work, it is thought that the observations in this paper will be useful if other districts are studied on similar lines. The peculiarity of Middlesex which makes it of special interest to the ecologist is the exceptionally

large proportion of its surface now covered with towns and villages. Few English counties can offer better opportunities for studying relict and vestigial floras and the various effects of man on the moss-vegetation. Though the modern flora is very much modified and reduced, the old records of mosses in literature, some of them dating from as far back as the eighteenth century, are relatively full, for Middlesex was until lately a favourite collecting ground of London botanists. From these some sort of an idea of the former flora can be obtained.

The present paper is the result of observations made from 1920 to 1927, begun with the object of writing a "local list." The method here adopted is to concentrate on certain specimen localities, as large parts of the county are so poor in mosses as not to be worth the trouble of careful working. Since most of the moss-vegetation here described will probably not survive the next twenty years, fuller records of the individual species than can here be given are desirable, so it is hoped to publish later a complete catalogue of Middlesex mosses.

The nomenclature used is that of the British Bryological Society's *Census Catalogue of British Mosses*, 2nd edition 1926, and Macvicar's *Student's Handbook of British Hepatics*, 2nd edition 1913.

The following abbreviations are used in the lists, etc.: v.a. = very abundant, a. = abundant, f. = frequent, o. = occasional, r. = rare, v.r. = very rare, l. = local, d. = dominant, s.-d. = subdominant. Where the areas considered are very small or the frequencies of the species are difficult to estimate correctly for some reason, merely their presence or absence is shown by means of the signs + and - respectively: (+) = a record not confirmed by the author; [+] = a record for a species certainly extinct in the locality in question; c.fr. = with sporogonia.

DESCRIPTION OF THE DISTRICT AND ITS VEGETATION.

As a full description of the county can be found in the Introduction to the *Flora of Middlesex* (3) and other works of reference, it is only necessary to give here a sufficient outline of its topographical, climatic and geological features and of its general vegetation, to make the subsequent matter intelligible.

Middlesex is the smallest but one of English counties. Its shape is an irregular parallelogram of which the Thames forms the base, into which a small tongue of Hertfordshire containing Barnet projects from the north. The longest straight line which can be drawn in it runs from Chertsey Bridge in the south-west to near Waltham Cross in the north-east, a distance of 28 miles (c. 45 km.) and its area is 281.5 sq. miles (c. 1087 sq. km). The river Colne forms the western boundary and the Lea the eastern, while the northern limit is artificial, but follows in part the south-eastern watershed of the upper Colne. Besides these rivers there are several smaller streams such as the Cran and Brent which like them also flow into the Thames, but rise within the county boundaries. The southern half of the county is a plain, sloping

down towards the Thames, but dead level only in its south-western portion. In this plain two hills stand out, Harrow Hill (373 ft. = c. 112 m.) and the "Northern Heights" of Hampstead and Highgate (highest point 440 ft. = c. 132 m.). The northern part of the county consists of low hills. A ridge of hills, broken here and there by gaps, follows the county boundary eastwards from its north-west corner at Harefield, passing out into Hertfordshire near Mill Hill. On this ridge is the highest point in the county (near Harrow Weald common, 504 ft. = c. 151 m.). The north-east of the district is an irregular system of low ridges of hills.

The climate is that typical of south-eastern England generally, that is, more continental than the western parts of the British Isles. The rainfall is low (mean annual c. 25 in. = c. 62.5 cm.). This fact, together with the absence of hard rocks, makes Middlesex a district in which an abundant and varied flora of bryophytes is not to be expected.

In its effect on the vegetation the most important characteristic of the county is the exceptionally large proportion of its surface which is built over. A large part of London lies within it (as the administrative county of London is included in Middlesex for the purposes of this paper) and even in the middle of the last century occupied one-sixth of its surface: the rest of the county is covered with towns, villages and suburbs, all increasing so rapidly that it will soon be possible to consider the whole of it as part of "Greater London." The country districts consist chiefly of grassland, but on the lighter soils, especially on the alluvium of the Thames and Lea valleys, the land is used for market gardening and fruit-growing. The amount of woodland and common land is very much less in proportion to the total area than in most of the neighbouring counties.

Clay is the most widespread soil in Middlesex and forms the surface soil of all the lower lands, except in the river-valleys and in the south-west. The slopes of the higher hills are also clayey. Most of this clay is the Eocene London Clay, but some belongs to the Reading and Woolwich series. The whole of the clay area is very poor in woods and consists mainly of small pastures bordered with elm trees and high hedges. The clayey district is naturally rather damp and streams and ponds are very frequent. The slightly undulating surface however prevents it from ever becoming very marshy. Though clay occupies a far larger area in Middlesex than any other soil, it only bears a small fraction of the total moss-flora and is incomparably poorer than the gravel soils. This is chiefly due to the fact that the gravel soils are unsuitable for cultivation and have been left undisturbed until lately, but clay soils always seem to have a far less varied moss-flora than sand or gravel, though observation of clay districts in other counties shows that it is not necessarily less abundant.

Sand is not a common soil in Middlesex. The Bagshot Sand which caps the hills of Harrow, Hampstead and Highgate is the only sandy soil which covers

any large area. Harrow and Highgate hills are almost completely built over, but Hampstead Heath still keeps some of its natural vegetation, though it has suffered much from its nearness to London. Gravel, which is ecologically a very similar soil to sand, is much more widespread. The top of the long ridge of hills along the north-west border of the county is covered with "Plateau" or "High Level" gravel of glacial origin and still has considerable relics of its "wild" vegetation. The same gravel covers the hills in the north-east of the county, where Enfield Chase, now disappeared, was situated. The Reading and Woolwich beds of Ruislip and Northwood also give rise to light soils and have quite large areas of semi-natural vegetation. Most of the vegetation on these light soils was probably *Quercetum sessiliflorae*, but there are also traces of a more heathy type of vegetation.

The chalk, which forms the soil of so much of the neighbouring counties, occurs in Middlesex only in two small tracts. One is about $3\frac{1}{2}$ miles long, but less than half a mile wide, following the western slope of the low hill on which Harefield stands: the other is a very small, irregular patch near South Mimms. Both consist chiefly of arable land and while neither of the two characteristic types of chalk vegetation, the chalk down and the chalk beechwood¹, is represented on them, their chalk-pits and chalky lanes have an interesting and comparatively rich bryophytic vegetation. Harefield and South Mimms are situated respectively in the extreme north-western and northern corners of the county and so both districts are still fairly rural.

DETAILED DESCRIPTION OF THE BRYOPHYTIC VEGETATION.

1. WOODLAND AND SCRUB.

The woodland forming the ancient "Forest of Middlesex" which is said to have once covered a large part of the county may be assumed to have been, at least originally, all oakwood². On the heavy clay this woodland was probably ordinary *Quercetum Roboris*, passing through an intermediate Oak-Hornbeam type on the loams derived from the Reading and Woolwich Beds and the lowest strata of the London Clay into *Quercetum sessiliflorae*. If the views of Salisbury (11) and others are correct, the comparatively small fragments of oakwood that still remain on the lighter soils are the direct, though modified descendants of this primitive woodland. Their bryophytic flora supports this view³. Some of the oakwoods on the sand and gravel have degenerated into birchwood or scrub, or birchwood has arisen from heathland probably originally derived from oakwood. On the heavy clay the only woods are some small copses from which no idea of the original bryophytic vegetation can be obtained. The absence of true chalk beechwood

¹ Park Wood, Harefield, a beechwood, is on chalk, but the ground vegetation is not characteristically calciphilous, owing to the depth of superficial non-calcareous soil.

² "The natural woods of this county probably consisted largely of oak as it is a prominent tree in the small portions of them that remain" (3, 264).

³ See p. 275, below.

has been referred to above (p. 272), but there is some reason for believing that there were once some non-calcareous beechwoods in the county of which Ken Wood is the chief relic.

Before going on to describe the moss-vegetation of the different types of woodland in detail, a short analysis of the structure of woodland moss-vegetation in general must be given, as most previous writers have not distinguished sufficiently clearly between the several communities that are present. Loeske (8, p. 93) however points out very well the distinctness of the two primary divisions of epiphytes and terrestrial bryophytes. One community is xerophytic, the other mesophytic, but they are united by another group inhabiting the bases of the tree-trunks, old logs and stumps, etc., as well as by being dependent on the same "Schutzpflanze." Loeske calls these communities "Untervereinen" (subassociations), but they correspond rather to the "strata" which are recognised in the phanerogamic flora of woodlands. A fourth stratum of mosses may be distinguished, which Loeske recognises but does not class with his other two, namely the terrestrial community on banks, cart-ruts, etc. (i.e. all non-horizontal surfaces of the wood-floor). The flora of this stratum is usually very distinct¹ from that of the level parts of the wood-floor. The main factor in differentiating between the two habitats is the tendency for dead leaves to accumulate on the level parts of the wood-floor during the season when the mosses are most active. Mosses suffer in competition more from smothering by the dead parts of higher plants in winter and spring than from shading by their leaves in summer. The effect of this factor is shown by the life-forms of the mosses in the two strata. On the level wood-floor the predominating form of moss is either the pleurocarpous growing in tufts which swell up when wet and allow the leaves to glide off (e.g. *Eurhynchium striatum*, *Hypnum cupressiforme*) or the tall, stiff acrocarpous type (e.g. *Polytrichum formosum*, *Mnium hornum*). On the banks the shorter carpet-forming acrocarpous type predominates (e.g. *Dicranella heteromalla*) and delicate plants like many of the Hepaticae are able to exist. As Loeske points out (8, p. 132), many mosses of the wood-floor have cuspidate or julaceous tips to their branches (e.g. *Hypnum Schreberi*, *Eurhynchium piliferum*) which help them to pierce the carpet of dead leaves much as the "spear-shoots" of some woodland flowering plants enable them to pierce the overlying soil. That the dead leaves are not the only factor in differentiating the two strata is shown by the fact that in places where the wood-floor is swept clear by the wind the moss-vegetation is not the same as on the banks, though a few bank species may occur there.

There are thus the following four strata in woodland moss-vegetation:

(i) The *first* on the trunks and branches of the trees, consisting of epiphytes with various xerophytic characters.

¹ In the pinewood on Oxshott Heath, Surrey, 13 species of bryophytes occur on the floor of the wood, 6 species on the banks and around rabbit-holes, but no species was common to both habitats.

(ii) The *second* on the tree-bases and stumps, consisting of various humus-loving epiphytic and terrestrial species.

(iii) The *third* on the wood-floor, mainly of tall terrestrial species.

(iv) The *fourth* on the woodland banks, consisting of more delicate terrestrial species.

The first stratum of mosses is quite absent at the present day in the Middlesex woods, though there are some old records of various epiphytes. This is a very general effect of a smoky atmosphere¹. It is interesting to note that Harrison and Garrett (6) used the presence or absence of arboreal mosses as a test of the purity of the atmosphere in experimental work on moths. In the typical arboreal genus *Orthotrichum* only the very abundant *O. diaphanum* is at all common in Middlesex, where it is chiefly found on walls. Another epiphytic species was found on elders at South Mimms but it was too stunted to identify. *Orthotricha* scarcely appear till 20–25 miles out of London (all Middlesex lies well within this radius) and not till near the edge of the Chiltern escarpment, where the rainfall is also greater, do they grow freely.

(i) *The Oak-Hornbeam Woods.*

The most important group of woods in the county lies on the low hills between Ruislip and Harefield. All these woods are of the oak-hornbeam type and very similar to the Hertfordshire woods described by Salisbury (11). Only the largest, Park Wood and Copse Wood, both of which are over a mile in length and less than a mile in width, were examined carefully. The soil of both woods is partly the loamy Reading and Woolwich Beds and at the highest point (293 ft. = c. 87.9 m.) in Copse Wood there is a patch of gravel, but it is mostly London Clay, which is here however largely of a loamy or even sandy character (basement beds). In the vegetation there is a complete gradation from the *Quercus Robur-Carpinus* coppice-with-standards on the heavy soils to the *Quercetum sessiliflorae* on the lighter, which has mostly been left as high forest. Under the hornbeam there is little undergrowth and deep shade, but the *Quercetum sessiliflorae* is much lighter and has an undergrowth of *Pteridium*, *Scilla nutans*, etc. Some houses have been built in the northern part of Copse Wood, with very harmful results to the surrounding vegetation. The light and heavy soils pass so insensibly into one another that in dealing with the mosses it has been found impossible to distinguish sharply between them, so in Table I a list of the bryophytes of the woods as a whole is given, while the species definitely restricted to one kind of soil are pointed out below.

The second stratum of the moss-vegetation at Ruislip is very well repre-

¹ The late E. B. Chamberlain wrote to the author, "There are within 20–30 miles of New York almost none of the tree-growing species, as *Ulota*, *Orthotrichum*, *Leskea*, etc. They were here 40 years back according to the collections of Mrs Britton and Austin." Many English local floras note the same fact. The similar effect on corticolous lichens is discussed in great detail by Wheldon and Travis (18).

sented. The old coppiced stumps of hornbeam in particular are thickly covered with moss. The most abundant species on both kinds of soil are *Hypnum cupressiforme* and *Eurhynchium Myurum*, on the heavy soils only *Eurhynchium praelongum*, on the lighter *Tetraphis pellucida* and *Dicranum scoparium*. *Tetraphis* seems to be characteristic of *Quercetum sessiliflorae* in English woodlands. Two rare species of *Dicranum*, *D. montanum* and *D. flagellare* occur in this stratum. The former occurs both in Copse Wood and Park Wood at the base of oak-trunks, very rarely on dead stumps: the latter grows almost entirely on dead stumps and rotten wood¹ and is very abundant in Park Wood, though it does not occur outside a strictly limited area. Both species occur in Britain chiefly in undoubtedly primitive woodlands.

The ground flora is rather irregularly distributed; where *Pteridium* is abundant, on the lightest soils, it is almost absent. The list of species is not very different on the two kinds of soil, but *Webera nutans*, *Hypnum cupressiforme* var. *ericetorum* and *H. Schreberi* are more abundant on the light soils, while *Eurhynchium piliferum* is confined to moist places on the clay. *Hylocomium squarrosum* and *Hypnum cuspidatum* occur among grass bypaths². The former species seems unable to live except in grass thick enough to form a turf. On heaths it only appears when they reach the grass-heath stage (cp. p. 284). The abundance of *Pleuroidium alternifolium* in Copse Wood and the adjoining land is remarkable as it has not been seen in Park Wood or elsewhere in Middlesex. Societies occur in damp places which are of very different character on the different types of soil. On the sandy soils *Calluna* occurs in them, associated with *Sphagnum*. The flora of the banks of woodland streamlets is dealt with below (Table III).

The fourth stratum is represented by the moss-carpet on banks by the side of tracks, in cart-ruts, etc. Hepatics are prominent in it, but are not as abundant or as varied as in some of the Hertfordshire woods.

Mimms Wood in the north-east of the county is very like these Ruislip woods, but most of it lies across the Hertfordshire boundary.

There is an important group of oak-hornbeam woods, fragments of a once large forest, on the Northern Heights between Hampstead and Highgate. Some of the original phanerogamic vegetation³ remains in a fairly natural state, but of mosses, no doubt owing to the smoky atmosphere of the neighbourhood, there are only comparatively small traces. The soil is here mainly Bagshot Sand⁴. In Ken Wood there are some ancient beeches which are probably native: the undergrowth is of planted *Rhododendron ponticum* and *Prunus Laurocerasus*. The old records of bryophytes indicate a rich flora, though now there is only a very impoverished sandy oakwood moss-vegetation. The old

¹ Thus confirming Dixon's observation (4, p. 118).

² This fact was also observed by Salisbury in Hertfordshire (11, p. 11).

³ An account of this is given by Tansley (14, pp. 92-100).

⁴ Cp. Tansley (14, p. 92 and footnote).

records together with the recent flora of Ken Wood, are given in Table I. Queen's Wood (or Churchyard Bottom Wood) in the same neighbourhood is given in the old records as a locality for *Trichocolea tomentella* which occurs in the Hertfordshire oak-hornbeam woods (11), and though most of the mosses have been destroyed by sweeping up dead leaves, *Fissidens taxifolius*, c.fr. occurred there abundantly in 1921. *Ptilidium ciliare* and *Haplozia sphaerocarpa* which, like *Trichocolea*, occur rarely in the oak-hornbeam woods of Hertfordshire (11) were found over a hundred years ago in Coldfall Wood, Finchley.

(ii) *Non-calcareous Beechwoods.*

There is scarcely any trace left of the large woods of Enfield Chase, cut down in the eighteenth century¹. The soil of the district is gravel and the records of the following epiphytic mosses, *Cryphaea heteromalla*, *Antitrichia curtipendula*, *Pterogonium gracile*, *Brachythecium plumosum*, some of which are stated to have grown on beeches, suggests that the woods were non-calcareous beechwood like that of Epping Forest and Burnham. There are some ancient beech trees still left in the neighbourhood. The presence of beeches in Ken Wood, referred to above, supports this theory.

(iii) *Birchwood.*

There are, on Stanmore and Harrow Weald Commons on the ridge of gravelly hills along the north-western boundary of the county, some good examples of the birchwoods (*Betuletum albae*, agg.) which are so characteristic of the commons around London. Though there are not many oaks on either common now, the presence of oakwoods in the adjacent private grounds makes it almost certain that *Quercetum sessiliflorae* once covered the land the birchwoods now occupy². The oakwoods however seem to have passed through an intermediate heath stage and not to have degenerated directly into birchwood. In 1869 Trimen and Dyer (3) spoke of Stanmore Common as "a fine open piece of heath" and De Crespigny in 1877 (1) describes it as "turfy and furze grown, except along the lines of drainage which are open and marshy," while Harrow Weald Common was then "a narrow strip of wet gravelly waste...without turf and of a less furzy character than the [Stanmore] Heath." When the present writer first visited Stanmore Common in the winter of 1920-21 it was mostly pure birchwood, with a small admixture of aspen (*Populus tremula*), oak (*Q. sessiliflora*) and *Pinus sylvestris*. On the borders of the several small streams which cross the common there was open boggy and marshy ground and the lower clayey parts were partly covered with an extremely dense thicket of blackthorn (*Prunus spinosa*). In the hot summer of 1921 some of the woods were burnt and in the following winter nearly all the trees were cut down except a few in the north corner of the common and a

¹ Trimen and Dyer (3, p. xxx).

² The old records of *Hylocomnium loreum* and *Leucobryum glaucum* support this assumption.

small piece of woodland in the eastern corner which is still standing (1927). The felled parts of the common are rapidly regenerating. Harrow Weald Common in 1921 consisted of various stages of birchwood and scrub: it suffered much less from fire and has changed very little in the whole seven years it has been observed. The development of birchwood on both commons between 1877 and 1921 is possibly due to the cessation of pasturing as the surrounding district has become less rural in character.

The standing birchwoods have an undergrowth of abundant brambles, sallows and other shrubs, with the usual herbaceous flora of sandy woodland.

The moss-flora is very abundant—a great contrast to that of the birchwoods near Berlin, where Loeske (8) describes it as being extremely poor. Unfortunately no full notes were made of the mosses in the woods cut down in 1921, so the list given in the table was drawn up chiefly from the woods of Harrow Weald Common and from those woods still remaining at Stanmore. The general character of the moss-flora is not unlike that of the Ruislip woods, but of a much more heathy character, this feature being shown especially in the occurrence of two species of *Campylopus*.

Even apart from the influence of smoke no tree stratum of mosses is to be expected on birch¹, but the second stratum is well represented. *Aulacomnium androgynum* is a conspicuous member of this community. It is much more abundant than in the Ruislip woods, but it is less plentiful in some years than others.

The ground flora is also abundant. *Webera nutans* is the most abundant species here and forms pure carpets sometimes one or two metres broad, fruiting plentifully. Where the wood-floor is grassy, the larger Hypnoid mosses, *Brachythecium purum*, *Hypnum cupressiforme* var. *ericetorum* and *Hylocomium squarrosum*, are conspicuous. Damp societies of two types occur in wet places. One type² corresponds to the damp societies with *Calluna* at Ruislip and occurs in damp hollows: the other, occurring in the stream valleys and in the numerous small gravel diggings, some of which contain permanent pools, has a vegetation consisting chiefly of low-acidity *Sphagna* (the acidity in these hollows is about pH 5).

The succession after burning at Stanmore was unfortunately not followed carefully in its early stages. For that reason and because nearly identical successions have already been described (13), the details will not be given here. The four main phases in the cryptogamic succession are:

(i) The *Funaria hygrometrica* carpets, with *Ceratodon purpureus* as a subsidiary species.

(ii) As the salts set free from the ashes are washed out of the soil, *Ceratodon* displaces *Funaria*.

¹ The writer saw one species of moss on birches in the New Forest. Loeske records 5 or 6 from birch-trunks near Berlin (8). West (17) records 4 bryophytes from birches in Carnarvonshire.

² This type is practically equivalent to wet heath.

Table I.

The Bryophytes of Middlesex Woodlands.

| Species | Localities | | |
|-----------------------------------|---|---|---|
| | Ruislip Woods (<i>Quercus Robur</i> , <i>Q. sessiliflora</i> , <i>Carpinus Betula</i>) | Hampstead Woods (<i>Q. sessiliflora</i> , <i>Fagus sylvatica</i>) | Stanmore and Harrow Weald Commons (<i>Betula alba</i>) |
| <i>Stratum I</i> (tree-trunks) | | | |
| <i>Frullania dilatata</i> | [+] | — | — |
| <i>Orthotrichum affine</i> | [+] | — | — |
| <i>Pterogonium gracile</i> | — | [+] | — |
| <i>Radula complanata</i> | [+] | — | — |
| <i>Ulotia crispa</i> | [+] | — | — |
| <i>Stratum II</i> (stumps, etc.) | | | |
| <i>Amblystegium serpens</i> | — | o. | — |
| <i>Aulacomnium androgynum</i> | o. | — | l.a. |
| <i>Brachythecium velutinum</i> | f. | v.r. | o. |
| <i>Bryum capillare</i> | r. | — | — |
| <i>Campylopus flexuosus</i> | — | — | l.a. |
| <i>Catharina undulata</i> | v.r. | — | — |
| <i>Cephaloziella byssacea</i> | v.r. | — | — |
| <i>Dicranella heteromalla</i> | o. | — | l.a. |
| <i>Dicranoweisia cirrata</i> | r. | — | — |
| <i>Dicranum flagellare</i> | l.a. | — | (v.r.) |
| <i>D. montanum</i> | l.f. | — | — |
| <i>D. scoparium</i> | f.—a. | — | r. |
| <i>Eurhynchium Myurum</i> | a. | — | — |
| <i>E. praelongum</i> | f.—a. | — | o. |
| <i>Hypnum cupressiforme</i> | a.—v.a. | v.r. | f |
| <i>Lepidozia reptans</i> | — | f. | — |
| <i>Lophocolea bidentata</i> | o. | — | o. |
| <i>L. cuspidata</i> | o. | — | — |
| <i>L. heterophylla</i> | f.—a. | v.r. | r. |
| <i>Mnium hornum</i> | o. | — | — |
| <i>Plagiothecium denticulatum</i> | o.—f. | — | o. |
| <i>P. latebricola</i> | r. | — | — |
| <i>P. sylvaticum</i> | o. | — | — |
| <i>Tetraphis pellucida</i> | l.a. | r. | — |
| <i>Webera nutans</i> | o. | — | f. |
| <i>Stratum III</i> (floor) | | | |
| <i>Haplozia crenulata</i> | l.f. | — | — |
| var. <i>gracillima</i> | l.f. | — | — |
| <i>Aulacomnium androgynum</i> | — | — | l.f. |
| <i>Barbula convoluta</i> | — | v.r. | — |
| <i>Brachythecium purum</i> | o. | — | l.a. |
| <i>B. rutabulum</i> | l.f. | o. | — |
| <i>Calypogeia fissa</i> | r. | — | — |
| <i>C. Trichomanis</i> | — | — | r. |
| <i>Campylopus flexuosus</i> | — | — | l.f. |
| <i>C. pyriformis</i> | — | — | o. |
| <i>Catharina undulata</i> | a. | — | l.a. |
| <i>Cephalozia bicuspidata</i> | r. | o. | — |
| <i>Cephaloziella byssacea</i> | r. | — | v.r. |
| <i>Dicranella heteromalla</i> | r. | l.a. | f. |
| <i>Dicranum scoparium</i> | f.—a. | — | f. |
| <i>Diplophyllum albicans</i> | v.r. | (+) | — |
| <i>Eurhynchium piliferum</i> | r. | — | — |
| <i>E. praelongum</i> | a. | — | o. |
| <i>E. striatum</i> | l.f. | — | — |
| <i>E. Swartzii</i> | o. | — | r. |
| <i>Hylocomium splendens</i> | v.r. | — | — |

Table I (contd.).

| Species | Localities | | |
|---|---|---|---|
| | Ruislip Woods (<i>Quercus Robur</i> , <i>Q. sessiliflora</i> , <i>Carpinus Betula</i>) | Hampstead Woods (<i>Q. sessiliflora</i> , <i>Fagus sylvatica</i>) | Stanmore and Harrow Weald Commons (<i>Betula alba</i>) |
| <i>Stratum III</i> (floor), contd. | | | |
| <i>Hylocomium squarrosum</i> | l.a. | — | o. |
| <i>H. triquetrum</i> | (+) | — | — |
| <i>Hypnum cupressiforme</i> | a. | r. | f. |
| var. <i>ericetorum</i> | l.a. | — | l.a. |
| <i>H. cuspidatum</i> | l.f. | — | — |
| <i>H. Schreberi</i> | l.a. | — | r. |
| <i>Lepidozia reptans</i> | — | r. | r. |
| <i>Lophocolea bidentata</i> | f. | — | o. |
| <i>L. cuspidata</i> | o. | — | — |
| <i>L. heterophylla</i> | o. | — | — |
| <i>Mnium hornum</i> | l.a. | f. | l.f. |
| <i>M. undulatum</i> | (+) | v.r. | — |
| <i>Plagiochila asplenoides</i> | (+) | — | — |
| <i>Plagiothecium denticulatum</i> | r. | — | — |
| <i>P. elegans</i> | — | — | o. |
| <i>P. sylvaticum</i> | — | v.r. | — |
| <i>P. undulatum</i> | (+) | (+) | [v.r.] |
| <i>Pleuroidium alternifolium</i> | l.a. | — | — |
| <i>Polytrichum formosum</i> | a. | v.r. | l.a. |
| <i>Scapania curta</i> | r. | — | — |
| <i>Thuidium tamariscinum</i> | l.f. | — | r. |
| <i>Tortula subulata</i> | (+) | — | — |
| <i>Webera nutans</i> | l.a. | — | a.—v.a. |
| Damp Societies. (a) With <i>Calluna</i> | | | |
| <i>Alicularia scalaris</i> | — | — | + |
| <i>Aulacomnium palustre</i> | — | — | + |
| <i>Calypogeia fissa</i> | — | — | + |
| <i>Campylopus pyriformis</i> | — | — | + |
| <i>Cephalozia bicuspidata</i> | — | — | + |
| <i>Gymnocolea inflata</i> | — | — | + |
| <i>Hypnum cupressiforme</i> var. <i>ericetorum</i> | + | — | — |
| <i>H. cuspidatum</i> | — | — | + |
| <i>H. exannulatum</i> var. <i>pinnatum</i> | — | — | + |
| <i>H. Schreberi</i> | — | — | + |
| <i>Sphagnum compactum</i> var. <i>squarrosum</i> | + | — | — |
| <i>S. crassicladium</i> | — | — | + |
| <i>Webera nutans</i> | — | — | + |
| (b) Without <i>Calluna</i> | | | |
| <i>Aulacomnium palustre</i> | — | — | + |
| <i>Bryum pallens</i> | + | — | — |
| <i>Hypnum cordifolium</i> | + | — | + |
| <i>H. fluitans</i> | — | — | + |
| <i>Polytrichum commune</i> | — | — | + |
| <i>Sphagnum auriculatum</i> var. <i>canovirescens</i> | — | — | + |
| <i>S. crassicladium</i> | — | — | + |
| <i>Stratum IV</i> (banks) | | | |
| <i>Alicularia scalaris</i> | l.a. | — | — |
| <i>Haplozia crenulata</i> | l.a. | — | + |
| var. <i>gracillima</i> | + | — | — |
| <i>Calypogeia fissa</i> | — | — | + |
| <i>C. trichomanis</i> | — | + | — |
| <i>Catharinea undulata</i> | + | — | — |
| <i>Cephalozia bicuspidata</i> | + | — | + |
| <i>Cephaloziella Starkii</i> | + | — | — |

* Only on Stanmore in pools on the clay near the lower edge of the common.

Table I (contd).

| Species | Localities | | |
|-----------------------------------|---|---|---|
| | Ruislip Woods (<i>Quercus Robur</i> , <i>Q. sessiliflora</i> , <i>Carpinus Betula</i>) | Hampstead Woods (<i>Q. sessiliflora</i> , <i>Fagus sylvatica</i>) | Stanmore and Harrow Weald Commons (<i>Betula alba</i>) |
| <i>Stratum IV (banks), contd</i> | | | |
| <i>Ceratodon purpureus</i> | + | — | — |
| <i>Dicranella heteromalla</i> | a.—f. | f.—a | v.a. |
| <i>Diplophyllum albicans</i> | + | — | l.a. |
| <i>Fissidens taxifolius</i> | — | — | + |
| <i>Fossombronia pusilla</i> | — | (+) | — |
| <i>Hypnum cupressiforme</i> | + | — | + |
| <i>H. cuspidatum</i> | +† | — | — |
| <i>H. Schreberi</i> | +† | — | — |
| <i>Lepidozia reptans</i> | — | — | + |
| <i>Lophocolea bidentata</i> | + | + | + |
| <i>L. heterophylla</i> | + | — | + |
| <i>Marchantia polymorpha</i> | — | + | — |
| <i>Mnium affine</i> | — | — | + |
| <i>M. hornum</i> | + | + | + |
| <i>Plagiothecium denticulatum</i> | + | — | + |
| <i>P. elegans</i> | — | + | + |
| <i>Polytrichum commune</i> | +† | — | — |
| <i>Scapania curta</i> | + | — | — |
| <i>S. irrigua</i> | l.a. | — | + |
| <i>S. nemorosa</i> | + | — | — |
| <i>Webera nutans</i> | + | — | a. |

† These species were found in cart-ruts only and belong doubtfully to this stratum.

(iii) *Polytrichum* carpets (*P. juniperinum* in dry places, *P. commune* in moist places). At this stage, which was that reached at Stanmore in 1927, there is not a continuous carpet, but a number of large patches of moss between the regenerating trees. As the trees, which were then about a metre high, grow to maturity a gradual return of the woodland bryophyta presumably takes place.

One feature of this succession is well marked at Stanmore, namely the persistence on stumps of the trees of the dominants of earlier stages in the succession. Thus in 1927, when the ground is covered with fruiting patches of the *Polytricha*, *Ceratodon* and *Funaria* are abundant on the cut and burnt birch stumps, associated with the "weed" mosses *Brachythecium rutabulum* and *Bryum capillare*. The burning also seems to have increased the dampness of the common as the *Sphagna* and *Aulacomnium palustre*, which formerly occurred only in small patches, have spread considerably¹.

(iv) *Scrub*.

The small square piece of scrub called Watt's Common at Harefield is the relic of a much larger common (Harefield Common) (3). It has probably been derived indirectly, like the Stanmore birchwoods, from *Quercetum sessiliflorae*. It is only about 700 by 450 ft. (c. 213 × 137 m.) and is situated on Plateau Gravel. It is much spoilt by rubbish-dumping. The present phanero-

¹ This may be due merely to the wet weather of the last few years.

gamic flora of this common is a dense tangle of brambles, blackthorn, willows, young oaks and birches, mixed with *Pteridium* and some other heath plants. As on the other gravelly commons of Middlesex, the surface is broken by many small pits, some of which are wet in summer as well as winter. The records of flowering plants for the old Harefield Common (there are unfortunately no old records of the mosses) indicate a true heath vegetation with some wet heath, but the present moss-flora resembles that of the Stanmore birchwoods. The old common may have consisted of both wood and heath as some of the Buckinghamshire commons still do. The mosses noted were:

| | | | |
|-------------------------------|----|------------------------------|------|
| <i>Ceratodon purpureus</i> | o. | <i>Hylocomium squarrosum</i> | a. |
| <i>Eurhynchium praelongum</i> | f. | <i>Hypnum Schreberi</i> | a. |
| <i>E. Swartzii</i> | f. | <i>Thuidium tamariscinum</i> | l.a. |
| <i>Hylocomium splendens</i> | f. | | |

And in the gravel pits: *Sphagnum cymbifolium* var. *glaucescens*, *S. crassicaudum* var. *intermedium*, *Polytrichum commune*, *Dicranum Bonjeani*, *Hypnum riparium*.

2. HEDGES.

In attempting to describe the woodland moss-vegetation it is useful to turn to the hedgebanks and hedgerows for data to supplement those obtained from the very small number of woods now remaining.

Here and there in the rural districts of the county there are old quiet lanes bordered by banks and neglected hedges. These lanes are however rapidly giving place to modern roads with fences or iron railings along which it is useless to look for mosses. On the clay scarcely any lanes now remain, but on the gravel and chalk there are several with a fairly rich and varied moss-vegetation. In the chalky lanes the hedgerow is formed by clipped beech and plants of the chalk scrub, such as hawthorn, and dogwood (*Cornus sanguinea*). The older hawthorns may have thick stumps like a coppiced hornbeam or hazel and on these epiphytes are found. The undergrowth of these hedges is fairly thick. On the gravel there is a hedgerow often of hawthorn or there may be no real hedgerow at all, merely a bank and a fence in front of which grow scattered bushes. There are sometimes long stretches of bank on which the only phanerogamic vegetation is trailing brambles and scattered tufts of fine grasses (e.g. *Deschampsia flexuosa*) and wherever the slope of the bank is sufficient there are the bare gravelly patches which are such a favourable habitat for bryophytes. There also old mossy stumps are often found.

The moss-vegetation of a hedge is in general the concentrated essence of the moss-vegetation of the corresponding type of woodland, though the relative frequencies of the species are somewhat different. A few species characteristic of the hedgebanks (e.g. *Bartramia pomiformis*) have not been observed in any of the Middlesex woods, but possibly occur in woods in other districts. The fourth stratum of the woodland mosses is naturally that most

Table II.

The Bryophytes of Middlesex Hedges.

| Species | Localities | | | | | | | |
|---|------------|-------|------|------|------|------|-------|------|
| | Gravel | | | | Clay | | Chalk | |
| | I | II | III | IV | V | VI | VII | VIII |
| <i>On shrubs and stumps</i> | | | | | | | | |
| <i>Amblystegium serpens</i> | - | - | + | - | + | - | - | - |
| <i>Anomodon viticulosus</i> | - | - | - | - | - | - | + | - |
| <i>Brachythecium populeum</i> | - | - | - | - | + | - | - | - |
| <i>B. rutabulum</i> | - | - | + | - | - | - | - | - |
| <i>B. velutinum</i> | + | - | + | + | - | - | + | - |
| <i>Bryum capillare</i> | + | - | - | - | - | - | + | - |
| <i>Camptothecium sericeum</i> | + | + | + | + | - | + | + | - |
| <i>Ceratodon purpureus</i> | - | + | - | - | + | - | - | - |
| <i>Dicranella heteromalla</i> | - | + | - | - | - | - | - | - |
| <i>Dicranoweisia cirrata</i> | + | - | - | - | - | - | - | - |
| <i>Eurhynchium confertum</i> | - | - | - | + | - | - | + | - |
| <i>E. praelongum</i> | + | - | + | + | - | - | + | - |
| <i>Homalia trichomanoides</i> | - | - | + | - | - | - | - | - |
| <i>Hypnum cupressiforme</i> | + | + | + | - | - | - | + | - |
| <i>Lophocolea heterophylla</i> | + | + | - | + | - | - | - | - |
| <i>Madotheca platyphylla</i> | - | - | - | - | - | + | + | + |
| <i>Metzgeria furcata</i> | + | - | + | - | - | + | + | + |
| <i>Mnium hornum</i> | - | + | + | + | - | - | - | - |
| <i>Neckera complanata</i> | + | - | - | - | + | + | + | + |
| <i>Orthotrichum diaphanum</i> | - | - | - | - | - | - | + | + |
| <i>Plagiothecium denticulatum</i> | + | - | + | - | - | - | - | - |
| <i>P. latebricola</i> | - | - | - | - | - | + | - | - |
| <i>P. sylvatica</i> | - | - | + | - | - | - | - | - |
| <i>Tetraphis pellucida</i> | - | + | + | - | - | - | - | - |
| <i>Tortula laevipila</i> | - | - | - | - | + | - | - | - |
| <i>T. muralis</i> | - | - | - | - | + | - | + | - |
| <i>Webera nutans</i> | + | + | - | - | - | - | - | - |
| <i>Zygodon viridissimus</i> var. <i>occidentalis</i> | - | - | - | - | - | - | + | - |
| <i>On the banks</i> | | | | | | | | |
| <i>Amblystegium serpens</i> | f. | - | - | - | - | o. | - | - |
| <i>Aulacomnium androgynum</i> | - | - | - | l.a. | + | - | - | r. |
| <i>Barbula rubella</i> | - | - | - | - | - | - | - | o. |
| <i>B. unguiculata</i> | r. | - | - | - | - | - | + | o. |
| <i>Bartramia pomiformis</i> | o.* | v.r.* | - | l.a. | - | - | - | - |
| <i>Brachythecium purum</i> | l.a. | - | - | v.r. | - | - | - | - |
| <i>B. rutabulum</i> | - | o. | - | o. | + | f. | + | a. |
| <i>B. velutinum</i> | - | - | - | f. | - | - | - | - |
| <i>Bryum capillare</i> | - | - | - | - | - | l.a. | - | - |
| <i>Calypogeia trichomanis</i> | - | r. | - | l.f. | - | - | - | - |
| <i>Catharinaea undulata</i> | l.f. | r. | f. | f. | - | v.r. | - | - |
| <i>Cephalozia bicuspidata</i> | - | - | - | f. | - | - | - | - |
| <i>Ceratodon purpureus</i> | l.a. | - | - | - | - | r. | - | - |
| <i>Dicranella heteromalla</i> | v.a. | v.a. | l.a. | f. | - | l.a. | - | - |
| <i>Dicranum scoparium</i> | - | l.a. | - | - | - | - | - | - |
| <i>Diplophyllum albicans</i> | - | - | - | r. | - | - | - | - |
| <i>Eurhynchium praelongum</i> | l.a. | o. | l.a. | a. | + | a. | + | l.a. |
| <i>E. Swartzii</i> | f. | - | - | - | + | - | + | a. |
| <i>Fissidens bryoides</i> | o. | - | l.a. | l.a. | - | f. | - | a. |
| <i>F. incurvus</i> | - | - | - | r. | - | - | - | r. |
| <i>F. taxifolius</i> | r. | - | l.f. | l.a. | - | a. | - | l.a. |
| <i>Hypnum cupressiforme</i> | - | a. | - | - | - | o. | - | - |
| var. <i>ericetorum</i> | - | r. | - | - | - | - | - | - |
| <i>Lophocolea bidentata</i> | - | f. | - | a. | - | o. | - | - |

* Could not be refound in 1927.

Table II (*contd.*).

| Species | Localities | | | | | | | |
|-----------------------------------|------------|----|------|-----|------|------|-------|------|
| | Gravel | | | | Clay | | Chalk | |
| | I | II | III | IV | V | VI | VII | VIII |
| <i>On the banks (contd)</i> | | | | | | | | |
| <i>Lophocolea heterophylla</i> | — | — | — | f. | — | f. | — | — |
| <i>Marchantia polymorpha</i> | — | — | v.r. | — | — | — | — | — |
| <i>Mnium affine</i> | r.* | — | — | r*. | — | — | — | — |
| <i>M. hornum</i> | l.f. | f. | a. | f. | — | — | — | — |
| <i>M. undulatum</i> | r. | — | l.f. | r. | — | — | — | — |
| <i>Phascum cuspidatum</i> | — | — | — | — | — | v.r. | — | l.f. |
| <i>Plagiothecium denticulatum</i> | a. | f. | o. | f. | + | l.f. | — | o. |
| <i>P. elegans</i> | — | r. | o. | f. | — | — | — | — |
| <i>P. sylvaticum</i> | — | — | — | o. | — | l.a. | — | — |
| <i>Polytrichum formosum</i> | r | o. | — | — | — | — | — | — |
| <i>Pottia truncatula</i> | — | — | — | — | — | — | — | l.f. |
| <i>Thuidium tamariscinum</i> | — | — | — | r. | — | — | — | — |
| <i>Tortula ruralis</i> | — | — | — | — | — | — | r.* | — |

* Could not be refound in 1927.

strongly represented in the hedges, but the second is represented by the epiphytes of the shrubs and coppiced stumps, and a few species of the woodland floor (third stratum) may occur. In less smoky districts than Middlesex the first stratum is represented by the epiphytes on the hedgerow trees. The various strata are however not as clearly defined in the hedges as in the woodlands and it is not practicable to make more than a separation into epiphytes and terrestrial moss-vegetation.

The dominant moss on the gravelly hedgebanks is *Dicranella heteromalla* which forms low deep-green carpets. Grey-green patches are formed by lichens (usually the common *Cladonias*) or by *Bartramia pomiformis*. This moss, which is confined in Middlesex to these gravelly banks, occurs there as a peculiar short and light-coloured form, unlike the type in general appearance.

The moss-vegetation of the chalky lanes is related, as might be expected, to that of the chalk beechwood, though a few very constant and abundant species of the beechwood (e.g. *Hypnum molluscum*, *Plagiochila asplenioides*) are absent. These species however belong to the third stratum of the woods, which is always that least well represented in the corresponding type of hedge vegetation. The two most constant members of the chalk hedge flora are both epiphytes, *Neckera complanata* and *Madotheca platyphylla*. Indeed the epiphytic bryophytes in the different types of hedge are far more constant and characteristic than the bank flora. These both occur also on the clay, but much less abundantly. *Anomodon viticulosus* is a moss almost strictly characteristic of, and often very abundant in, chalk hedges and beechwoods in south-eastern England. It now only occurs in one locality on the Middlesex chalk. There is however one old record for it from a lane on the clay.

Thus, though the moss-vegetations of chalk and clay closely resemble one another, that of the gravel is entirely distinct.

Table II gives the flora of eight hedges on different soils. The localities are as follows:

1. Lane near South Mimms (loamy Reading and Woolwich Beds with some gravel).
2. Wood Lane, Brockley Hill (Plateau Gravel).
3. Road near Batchworth Heath (Plateau Gravel).
4. Lane near Harefield (Plateau Gravel and loamy Reading and Woolwich Beds).
5. Colindeep Lane, Hendon (London Clay, with some lighter soil).
6. Abandoned lane near Edgwarebury (London Clay).
7. Portion of lane between South and North Mimms (Chalk).
8. Various lanes near Harefield (Chalk).

No. 3 is rather damper and shadier than the other gravelly lanes. The list for No. 5 was taken from a single old stump and from a short stretch of bank. Both have since been destroyed by building operations.

3. HEATHS AND BOGS.

There seem to have been formerly quite considerable tracts of heathland in Middlesex, both in the north, from Harefield to Hampstead, and in the south at Hounslow, but of all of them only the smallest vestiges remain. Some disappeared during the enclosures at the beginning of the last century¹, others have in some way become covered with birchwood or scrub (cp. p. 276). There still exist however relics of heath at Stanmore, Ruislip ("Poor's Field"), Hampstead and Hounslow. All these heaths, except Hampstead which is on sand, are situated on gravel soils. No doubt these heaths were once covered by *Callunetum*, but continual traffic has changed them to grass-heaths². *Calluna* is now a comparatively rare plant in the county, yet on several of these grass-heaths small clumps or patches of it remain, which, as will be shown, form very effective refuges for the cryptogamic flora of the vanished *Callunetum*. Wet heaths, which were formerly well developed on the ground at the junction of the sand or gravel and the underlying impermeable London clay, are still more scantily represented in the modern vegetation.

In old undisturbed *Callunetum* very few species of mosses or lichens occur (though these are fairly abundant), because the competition of the tall, thickly growing *Calluna* is too great for any but a few robust species to stand. On the change from *Callunetum* to grass-heath the degenerating *Calluna* bushes become small and thin, small spaces of bare peat appearing between them. The bryophytes and lichens at once become more varied and abundant. This change is admirably described and illustrated by Farrow in his work (5) on the Breckland heaths, where however it is due, not as in Middlesex to traffic, but to the cropping of rabbits. Thus, on Oxshott Heath, Surrey, only three

¹ Cp. Trimen and Dyer (3, p. xxix).

² Cp. Tansley (15, p. 105).

species of mosses and four of lichens occur in the tall *Callunetum*, while five species of mosses, one hepatic and nine lichens occur in the degenerating *Callunetum*. Farrow ascribes a large part to the cryptogams in the final destruction of the *Calluna*, but where the degeneration is caused by traffic their effect is probably not appreciable. When the grass-heath stage sets in, this great development of mosses and lichens is suddenly checked by the growth of a closed turf of tufted heath grasses, whose competition is more serious even than that of *Calluna* in its best days. Thus it comes about that while the grass-heath is far richer than the *Callunetum* in flowering plants, it is very much poorer in bryophytes and lichens. Those patches of *Calluna* still left in Middlesex being in the second stage, it would be expected that their cryptogamic flora would be fairly rich, and this is true to a remarkable degree, in spite of their very small size.

The best of these patches of *Calluna* is that on Stanmore Common, in its south-west corner. It is about 500 by 200 ft. (c. 152×60 m.) in extent and is divided into two very unequal portions by a lane. The larger borders the Stanmore Cricket Ground and suffers much from trampling by crowds, as well as from mowing with scythes. The *Calluna* is very low-growing and there are many bare peaty patches, except on the margin of the grass-heath, where the heath grasses appear to be invading the *Callunetum*.

The bryophytes of this patch are:

| | |
|--|------------|
| <i>Cephaloziella byssacea</i> (on bare peat) | |
| <i>Ceratodon purpureus</i> | |
| <i>Dicranum scoparium</i> (the most abundant sp.) | |
| <i>Hypnum cupressiforme</i> var. <i>ericetorum</i> | } abundant |
| <i>H. Schreberi</i> | |
| <i>Polytrichum juniperinum</i> | |
| <i>P. piliferum</i> | |
| <i>Ptilidium ciliare</i> | |
| <i>Webera nutans</i> | |

With the lichens (all rather dwarfed and scanty):

| | |
|---------------------------|--------------------------|
| <i>Cetraria aculeata</i> | <i>Cladonia pyxidata</i> |
| <i>Cladonia coccifera</i> | <i>Lecidea uliginosa</i> |
| <i>C. furcata</i> | |

Ptilidium is a very interesting occurrence; though very rare in the London district, it was recorded long ago from another locality in Middlesex (p. 276) and it is very abundant in the *Callunetum* of North Germany¹. *Cephaloziella byssacea*, though often scarce and hard to find, is a very constant species of English *Callunetum*. It is very remarkable that such a tiny patch of *Calluna* as this should have so many of the bryophytes that are found on *Calluna* heaths even of great extent².

¹ (8) Rakete (10) speaks of it as forming "Massenvegetation" among *Calluna* in clearings in the pinewoods of Ober-Lausitz.

² English dry *Callunetum* is very poor in number of species. Loeske (8) records many more for *Calluna* heaths round Berlin, but he says only a few of these occur constantly.

On the neighbouring grass-heath bryophytes are scarce and the species occurring are quite different:

Brachythecium albicans
B. purum (among *Salix repens* only)
Ceratodon purpureus
Dicranum scoparium
Hypnum cupressiforme

Hylocomium squarrosum
 Lophocolea bidentata (among *Salix repens* only)
 Polytrichum juniperinum
 Webera nutans

Some scattered patches and small groups of *Calluna* bushes occur here and there on the grass-heath called the "Poor's Field," near Ruislip, chiefly on the banks flanking a cart-track. The plants of *Calluna* are more scattered and more closely invaded by grass-heath plants than they are at Stanmore and it is not practicable to distinguish sharply between the bryophytes of the *Callunetum* and those of the grass-heath. The species confined to *Calluna* clumps are marked with an asterisk in the following list. On the grass-heath itself mosses are mostly limited to places where the turf has been worn thin on the edge of the path which crosses the field or to the cart-ruts and other steep sandy banks. Where *Hypnum Schreberi* occurs elsewhere than among *Calluna* it probably marks the site of vanished *Calluna* bushes, as it seems unlikely that it could ever establish itself *de novo* in the dense turf of the grass-heath. There are a number of patches of *Ulex nanus* in the field in which, though the conditions seem like those in *Calluna* patches, no bryophytes occur. The species observed were:

Brachythecium albicans l.a.
 B. purum l.a.
 *Cephalozia byssacea (among *Dicranum scoparium* var. *orthophyllum*) v.r.
 Ceratodon purpureus f.
 Dicranum Bonjeani r.
 D. scoparium var. orthophyllum l.a.
 Hylocomium squarrosum l.a.
 Hypnum cupressiforme o.
 *var. ericetorum l.f.
 H. Schreberi l.a.
 Polytrichum formosum l.a. (in broad patches)
 P. juniperinum l.a.
 P. nanum r.
 P. piliferum l.f. } near cart-track only

With the lichens:

- **Cladonia fimbriata*
- **C. furcata*
- **C. pyxidata*

***Lecidea uliginosa**
Peltigera canina

Brachythecium albicans is strictly characteristic of grass-heath in Middlesex.

An interesting society occurs in the damp hollows in this field where *Carex flacca*, *Scabiosa succisa*, *Genista anglica* and other damp-loving plants occur. The facies of the bryophytic vegetation of this society is very unlike that of typical wet heath, perhaps because there is a large proportion of clay in the soil. The acidity is about pH 5. No *Sphagnum* occurs, but *Aulacomnium palustre* is very abundant. Its abundance varies from year to year: in 1923 it was so abundant as to make conspicuous yellowish-green patches in

the dull green turf. An almost precisely similar patch occurs in the valley of a stream on Stanmore Common. The soil here too is clay, but it is overrun by acid drainage water from above. The most striking peculiarity of both of these pieces of vegetation is the occurrence of *Hypnum molluscum* on an acid soil with a very low lime-content¹. At Stanmore this moss grows mingled with *Erica Tetralix* and *Calluna* and close to a patch of *Sphagnum*. It is usually considered one of the most calciphilous of British mosses (16, p. 192) and the present writer knows of no localities for it in the London district except these two which are not on the chalk. *Fissidens adiantoides*, which is associated with *Hypnum molluscum* both at Ruislip and at Stanmore, is also a chalk-grassland moss, but it also occurs commonly in very wet places such as bogs and fens. The following table gives the flora of these two patches:

| | Ruislip | Stanmore |
|---|---------|----------|
| <i>Amblystegium filicinum</i> | + | - |
| <i>Aneura pinguis</i> | - | + |
| <i>Aulacomnium palustre</i> | + | + |
| <i>Bryum pallens</i> | - | + |
| <i>Climacium dendroides</i> | - | + |
| <i>Dicranum Bonjeani</i> | + | + |
| var. <i>rugifolium</i> | + | - |
| <i>Fissidens adiantoides</i> | + | + |
| <i>Hylocomium splendens</i> | - | + |
| <i>Hypnum cuspidatum</i> | + | + |
| <i>H. molluscum</i> | + | + |
| <i>H. stellatum</i> var. <i>protensum</i> | + | + |
| <i>Philonotis fontana</i> | + | - |
| <i>Scapania undulata</i> | - | + |
| <i>Sphagnum auriculatum</i> var. <i>canovirescens</i> | - | + |
| <i>S. crassicaule</i> var. <i>intermedium</i> | - | + |
| <i>Thuidium tamariscinum</i> | + | + |

A vestigial grass-heath is found at the bend in the lane leading from Stanmore to Whitechurch. Mosses are found chiefly on the bare soil on top of ant-hills. The following species occur there: *Ceratodon purpureus*, *Polytrichum juniperinum*, *Hypnum cupressiforme*, *Dicranum scoparium*.

There is a considerable tract of heath on the Bagshot Sands of Hampstead. Much of this was formerly covered with *Callunetum* (15), but traffic has converted such heathland as remains into grass-heath and *Calluna* is all but extinct. The ground has been worn quite bare of vegetation in many places: in others the heath vegetation has been replaced by a "weed-grass" association (cp. 15). In fact, considering the enormous traffic which passes over it daily, it is remarkable how much of its original flora this heath preserves.

The records in the old books of such species as *Polytrichum aloides*, *P. piliferum*, *Dicranella cerviculata*, *Rhacomitrium lanuginosum*, *R. canescens*

¹ Since the above was written it has been discovered that a small part of the Ruislip bog has soil with a fairly high lime-content and that *H. molluscum*, *A. filicinum* and *F. adiantoides* are limited to this part. The reaction to hydrochloric acid of soil from beneath a tuft of *H. molluscum* at Stanmore was however almost imperceptible.

and *Bryum atropurpureum*, clearly indicate a moss-flora like that of the Surrey heaths, but all these species no doubt disappeared when the Callunetum was supplanted by grass-heath, as none of them have been seen for years. On the modern heath however mosses are very scarce and only *Campylopus pyriformis*, *Ceratodon purpureus*, *Webera nutans*, *Hypnum cupressiforme* with var. *ericetorum* and *Hylocomium squarrosum* are found. The last with *Brachythecium purum*, another very constant grass-heath plant, occurs among grass in Golder's Hill Park, on the borders of Hampstead Heath. The sandy banks of this area have kept their characteristic flora far more completely than the rest of the heathland.

On the West Heath at Hampstead there is still a patch of wet ground which is the remains of a bog well known to London botanists from the time of Gerard onwards. Though this patch lies in an enclave of country among the suburbs, several interesting relics of its old flora are still to be found on it. The most abundant flowering plants are *Eriophorum polystachion*, *Carex panicea* and *Molinia coerulea*. The following old records probably refer to this bog: *Aulacomnium palustre*, *Philonotis fontana*, *Hypnum fluitans*, *H. stramineum*, *Polytrichum commune*, *Sphagnum cymbifolium*, *S. acutifolium* [agg.], *S. fimbriatum*, *Aneura multifida*, *Cephalozia connivens*. The following species have been observed there recently: *Sphagnum cuspidatum*, *S. fallax*, *S. innundatum*, *Hypnum fluitans*, *H. stramineum*, *Gymnocolea inflata*, *Cephalozia bicuspidata*. The abundance of these species fluctuates from year to year in an extraordinary manner, as shown in the following table:

| | <i>Sphagnum cuspidatum</i> | <i>S. fallax</i> | <i>S. innun- datum</i> | <i>Hypnum fluitans</i> | <i>H. stramineum</i> | <i>Gymnocolea inflata</i> | <i>Cephalozia bicuspidata</i> |
|---------|--------------------------------|--------------------------------|-------------------------------|-----------------------------|-------------------------|-------------------------------|-----------------------------------|
| Winter | | | | | | | |
| 1920-21 | Not seen | One large tuft | Not seen | Abundant | One small tuft | — | — |
| Summer | | | | | | | |
| 1921 | " | A few thread- like plants | " | Decreasing | A few small plants | — | — |
| 1922 | " | None visible | " | Two or three small tufts | None visible | — | — |
| 1923 | " | " | " | " | " | — | — |
| 1924 | " | " | " | " | " | — | — |
| 1925 | — | — | — | — | — | — | — |
| 1926 | One tuft | A healthy tuft in same spot | Not seen | Frequent | None visible | Frequent | Frequent |
| 1927 | Tuft much spread | Tufts much in- creased | A small healthy tuft found | Abundant | A small healthy tuft | Abundant | " |

Unfortunately no observations were made on the hepatics of the bog till 1926. The bog was not examined in 1925. During the period when the *Sphagna* were apparently extinct, many careful searches were made for them without finding the slightest trace. The cause of its sudden disappearance was the drought in the summer of 1921 and of its reappearance the succession of wet years since 1922. Under the unfavourable conditions of this district these mosses live on a very delicate balance of competition with the flowering plants, so that quite small differences in weather have an exaggerated effect on their abundance. Smaller fluctuations probably occur normally in the

abundance of mosses in bogs, though there are no definite observations to prove the fact.

There is now no common to represent the formerly extensive Hounslow Heath in the south of the county, all of it having been converted into drilling-grounds, fields, gravel-pits, etc. A field however was found near the site of the old heath on which gravel waste had been tipped and vegetation of a grass-heath character had grown up. This vegetation cannot of course be lineally descended from the old vegetation of Hounslow Heath. Mosses are fairly abundant, especially on top of the overgrown mounds of gravel, and they are nearly all typical grass-heath species: *Catharinea undulata*, *Polypodium juniperinum*, *P. piliferum*, *Dicranum scoparium* var. *orthophyllum*, *Ceratodon purpureus*, *Mnium affine*, *Hypnum cupressiforme*, *Brachythecium purum*, *Hylocomium squarrosum*, *Webera nutans*, *Lophocolea bidentata*.

4. GRASSLAND AND MARSH.

Like alluvial water-meadows, the clay meadows have scarcely any moss-flora. The grasses grow long and rank and even the most robust bryophytes have little chance of competing with them. Pastures in which the grass is kept short by animals are richer in mosses than hay-fields, but *Eurhynchium praelongum*, *Brachythecium rutabulum* and *Hypnum cuspidatum* are the only species commonly found in them and even they are usually thin and thread-like in habit. These species with *Fissidens bryoides* often occur in lawns in rather damp London gardens. In clay marshes mosses are no more plentiful, except that *Hypnum cuspidatum* is sometimes abundant. *Bryum pallens* has been recorded from this habitat.

There probably never was any natural chalk grassland in Middlesex, but a moss-vegetation of some interest is found in the chalk-pits at Harefield. Pits which are still being actively quarried of course have no mosses, but in old disused ones they are often abundant. In Middlesex many of the old pits have been used as rubbish-tips or fowl-runs and only "weed-mosses" (e.g. *Funaria hygrometrica*, *Eurhynchium Swartzii*) then occur in them. The South Mimms pits have been spoilt in the same way. In parts of the larger pits at Harefield, and in a very small disused pit at Springwell in the same neighbourhood the moss-vegetation is similar to that in chalk-pits of the neighbouring counties.

The moss-vegetation of chalk-pits is closely related to that of chalk grassland. On chalk downs two groups of mosses are found, one of tall species in level places where the turf is close, the other of smaller species growing between the tussocks on steep slopes where the turf is broken into tufts or terraces. The second of these forms most of the moss-vegetation of chalk-pits, but some old pits have a level grassy floor where the first group may predominate. The larger chalk-pits have vertical chalk-cliffs which are only colonised by

one species, the well-known *Seligeria calcarea*. This is so abundant in several of the Harefield pits as to colour whole expanses of the cliff brown when it is in fruit. *Hypnum molluscum* is the dominant moss on the detritus slopes. Its occurrence on the clay has been alluded to and shows the same affinity between chalk and clay floras as was found to obtain in the hedge floras. No hepatics occur in the Middlesex chalk-pits, for they are characteristically absent¹ on chalk grassland.

The following species were observed in Harefield chalk-pits:

Floor

Brachythecium rutabulum v.a.
B. purum v.a.
H. molluscum a.

Hypnum cupressiforme o.
Hypnum cuspidatum o.

Detritus slopes

Barbula unguiculata (c.fr.) r.
Camptothecium lutescens r.
Dicranella varia a.
Eurhynchium Swartzii l.a.

Fissidens adiantoides (?) r
Hypnum chrysophyllum †
H. molluscum v.a.

Cliffs

Seligeria calcarea (also on a loose lump of chalk) v.a.

5. DITCHES, BANKS, BARE SOIL AND ARABLE LAND.

In all the habitats so far dealt with (excepting the fourth stratum of woodland) the bryophytes have been wholly subordinate to the flowering plants and have had probably little or no influence on the vegetation as a whole. In the remaining terrestrial habitats however bryophytes form the dominant, and sometimes the only, vegetation. Their dominance may be permanent, as on banks and sides of ditches which are too steep to be successfully colonised by flowering plants, or it may be only temporary, as on bare soil and arable land where the flowering plants have not had time to oust the more quickly developing bryophytes. In the first group of habitats the bryophytic vegetation is perennial and the species composing it are also mostly perennials: in the second the vegetation lasts for a few weeks or months only and the species are either perennial mosses coming from other habitats which never reach maturity or small ephemerals which pass through their whole life-history in a very short time.

(i) *Banks and ditches* (Perennial communities).

In these habitats a primary division must be made according to the soil, but when more data are available from a wide area a division into a wet type and a dry may be necessary. The moss communities of ditches and banks are closely related to the fourth stratum of woodland moss-vegetation, indeed the latter is really only a special type of the former. Salisbury's "Cryptogamic Society" on the sides of woodland streamlets in Hertfordshire (11,

¹ *Lophozia badensis* occurs not uncommonly in small quantity on chalk-downs and in chalk-pits. About six other hepatics occur rarely on downs in the South of England.

p. 42) belongs to the damper type of bank community. A similar society occurs in the Middlesex oak-hornbeam woods (see Locality 10, Table III).

The division according to soil is a very sharp one. *Webera carnea* is characteristic of the damper type of clay bank, the genus *Fissidens* of the drier. On lighter soils *Dicranella heteromalla* is very constant and abundant, but not strictly characteristic. *Calypogeia fissa* is characteristic of sandy banks and of the fourth stratum of sandy and gravelly woodlands.

Table III.

The Bryophytic Vegetation of Middlesex Banks and Ditches.

| Species | Localities | | | | | | | | | |
|--------------------------------|------------|------|------|---|------|------|---------------|---|---|----|
| | Clay | | | | | | Loam and Sand | | | |
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| <i>Amblystegium filicinum</i> | - | - | - | - | a. | - | - | - | - | - |
| <i>A. serpens</i> | - | f. | f. | - | o. | - | - | - | - | - |
| <i>A. varium</i> | - | - | - | - | - | v.r. | - | - | - | - |
| <i>Haplozia crenulata</i> | - | - | - | - | - | - | - | - | + | - |
| <i>Barbula unguiculata</i> | - | - | o. | - | - | - | - | - | - | - |
| <i>Brachythecium rutabulum</i> | - | d. | d. | - | - | - | + | - | - | - |
| <i>Calypogeia fissa</i> | - | - | - | - | - | - | - | + | + | + |
| <i>Catharinaea undulata</i> | - | - | l.a. | + | - | - | - | - | + | + |
| <i>Cephalozia bicuspidata</i> | - | - | - | - | - | - | - | - | + | + |
| <i>Ceratodon purpureus</i> | - | - | - | - | - | - | - | - | + | - |
| <i>Dicranella heteromalla</i> | - | - | - | + | - | - | - | + | + | + |
| <i>D. varia</i> | - | - | - | - | r. | a. | - | - | - | - |
| <i>Eurhynchium praelongum</i> | a. | - | s.d. | - | - | - | + | - | - | - |
| <i>E. speciosum</i> | - | - | - | - | l.a. | - | - | - | - | - |
| <i>E. Swartzii</i> | f. | - | f. | - | - | - | - | - | - | - |
| <i>Fissidens bryoides</i> | d. | - | a. | - | r. | - | + | - | - | - |
| <i>F. exilis</i> | r. | - | - | - | - | - | - | - | - | - |
| <i>F. incurvus</i> | l.a. | - | - | - | - | - | - | - | - | - |
| <i>F. taxifolius</i> | o. | - | - | - | - | - | - | - | - | - |
| <i>Hypnum cuspidatum</i> | o. | - | - | - | - | - | - | - | - | - |
| <i>Lophocolea bidentata</i> | - | - | - | - | - | - | - | - | - | + |
| <i>Lunularia cruciata</i> | - | - | - | - | l.a. | - | + | - | - | - |
| <i>Pellia epiphylla</i> | - | - | - | - | - | - | - | - | + | + |
| <i>P. Fabbroniana</i> | - | - | - | - | l.a. | - | - | - | - | - |
| <i>Physcomitrium pyriforme</i> | - | r. | - | + | - | - | - | - | - | - |
| <i>Pleuridium axillare</i> | - | - | - | - | - | - | - | - | + | - |
| <i>Pottia truncatula</i> | o. | l.a. | - | - | - | - | - | - | - | - |
| <i>Sphagnum auriculatum</i> | - | - | - | - | - | - | - | - | - | + |
| <i>Tetraphis pellucida</i> | - | - | - | - | - | - | + | - | - | - |
| <i>Thuidium tamariscinum</i> | - | - | - | - | - | - | - | - | - | + |
| <i>Webera carnea</i> | - | - | - | + | o. | a. | + | - | - | - |
| <i>W. nutans</i> | - | - | - | - | - | - | - | - | + | - |
| <i>W. proligera</i> | - | - | - | - | - | - | - | + | * | - |

* Could not be found again in 1927.

Table III shows the vegetation of a number of banks and ditches in Middlesex. The localities are as follows:

1. Bank on edge of Monk's Mere, Hendon (London Clay).
2. Bank on Hampstead Heath Extension (London Clay).
3. Ditch on edge of field, South Mimms (London Clay).
4. Banks of streams and ditches on the East Heath and on Highgate Fields (London Clay).

5. Banks by the Thames, near Shepperton (Clay).
6. Bank by Penton Hook Backwater (Clay).
7. Ditches on the roadside at Breakspears, Harefield (Loam).
8. Banks by a pond, Little Stanmore (Sandy Loam).
9. Banks on the East and West Heaths, Hampstead (Bagshot Sands).
10. Banks of woodland streamlet in Park Wood, Ruislip (Loam).

Nos. 4, 5, 6, and 10 are banks of a damper type than the others; the soil of No. 6 is peculiar in having a high lime-content owing to the numerous remains of water-snails' shells embedded in it, hence the abundance of the calciphilous *Dicranella varia* there.

(ii) *Bare soil and arable land* (Ephemeral communities).

These habitats have a very distinctive and interesting flora. In them alone are found the so-called "earth-mosses," minute forms with a very simple organisation. Unfortunately in Middlesex bare soil is not often left undisturbed and therefore very few examples of ephemeral communities have been found. The bare patches on which they develop are of two types, (i) arable or other dry land left bare by the thinning out or dying away of its phanerogamic vegetation, (ii) mud left bare by the drying up of ponds or rivers. In the first group of habitats the moss-vegetation is necessarily mainly a winter community, reaching its maximum development about February, though patches of bare ground are occasionally found even in late summer with a vegetation of ephemeral mosses. In the second the moss vegetation usually grows up at the end of the summer, but then only in fairly dry summers: it is more shortlived even than the winter community.

Table IV.

Winter ephemeral community.

| Species | Locality | | | | |
|---------------------------------|-----------------------------------|--------|--------|--------------------------------|---------------------------|
| | Disused allotment gardens, Hendon | | | Clover field, New Year's Green | Bare sand, Ruislip Common |
| | 1922-3 | 1923-4 | 1925-6 | | |
| <i>Acaulon muticum</i> | + | - | - | + | - |
| <i>Barbula unguiculata</i> | - | - | - | - | + |
| <i>Brachythecium rutabulum</i> | - | - | - | + | - |
| <i>Bryum atropurpureum</i> | - | - | - | - | + |
| <i>Ceratodon purpureus</i> | + | + | + | - | + |
| <i>Phascum cuspidatum</i> | + | - | + | + | + |
| <i>Pleuridium alternifolium</i> | - | + | + | + | - |
| <i>P. subulatum</i> | - | - | - | - | + |
| <i>Pottia minutula</i> | - | - | - | - | + |
| <i>P. truncatula</i> | + | + | - | + | + |
| <i>Webera carnea</i> | + | + | + | + | - |

The flora of bare soil of the first type varies much from year to year. The preceding table shows the flora of such ground at Hendon in four successive years. In the third winter no ephemeral community developed in the original

spot owing to the formation of a nearly closed turf of grass, but in the fourth year one was found on a neighbouring piece of ground. The flora of two other pieces of bare ground, with a more sandy soil than the Hendon locality, is also given.

Ephemerum serratum, a very characteristic moss of the winter community on clay, has been twice recorded for Middlesex.

On some waste ground at Hendon a summer ephemeral community was found in August 1926. The species occurring were:

Aneura sinuata var. *major* (in damp spot)
Barbula unguiculata
Bryum argenteum
Eurhynchium praelongum

Eurhynchium Swartzii
Funaria hygrometrica
Hypnum cuspidatum.
Leptobryum pyriforme

Most of these species were undeveloped and none of them are true ephemerals.

Only one good example of the summer ephemeral community on mud has been met with in Middlesex. This was found in dried-up puddles in a disused lane near Edgwarebury. The species occurring were *Pleuridium axillare*, *Pottia truncatula* (not fruiting), *Physcomitrella patens*, *Webera carnea* and *Mnium undulatum* (a very young plant). On mud by the Penton Hook Backwater *Physcomitrella patens* was found growing in small scattered tufts in August 1926 when the water-level was low: it has also been recorded from mud by the Colne.

Various rare mosses such as *Nanomitrium tenerum* and *Physcomitrium sphaericum* have been recorded in this habitat from neighbouring counties, but *Physcomitrella patens* seems to be the most constant species.

6. AQUATIC HABITATS.

The natural and artificial bodies of water in Middlesex may be classified for ecological purposes as (i) ponds, (ii) rivers and canals, (iii) brooks, all of which flow more or less slowly. These habitats correspond to the "subformation of slowly moving waters relatively rich in mineral salts, (a) nearly stagnant waters and (b) slowly flowing waters" and the "subformation of quickly flowing streams" respectively, of *Types of British Vegetation* (14). Under these headings will be included the bryophytes of the various marginal habitats as well as the truly aquatic associations, as the former cannot be sharply marked off from the latter.

There are very numerous artificial ponds in Middlesex: in the clay lowlands almost every field has a small pond for the cattle and larger ponds made for various purposes are also plentiful, but there are no natural ponds or lakes. The only rivers of any size are the Thames and its tributaries the Colne and Lea, but there are several canals. Brooks are frequent in Middlesex but are often much polluted.

(i) *Ponds.*

Only one species occurs floating in ponds. This is the well-known *Riccia fluitans*¹. It prefers the small cattle ponds in which *Glyceria fluitans* is abundant. The water of these is often completely hidden by thick rosettes of *Riccia* mixed with *Lemna trisulca* and *L. minor*. At the end of the warm and very dry August of 1926 *Riccia* was found growing on mud at the edges of ponds, but these were merely plants stranded by the sinking of the water-level, not the rooting and truly terrestrial form (the var. *canaliculata* Hüb.). *Riccia fluitans* is fairly widespread but not very common in Middlesex. Among the rushes and grasses on the edge of such ponds various *Hypna* are found, which live submerged, or nearly so, for most of the year in an average season. The most widespread species are *H. cuspidatum*, forms of *H. fluitans*, and *H. aduncum*, but *H. giganteum* occurs in a pool at Stanmore Marsh. On stones and wood on the edge of ponds such mosses as *Amblystegium serpens*, rarely *A. filicinum*, *Eurhynchium confertum*, *Hypnum riparium* and var. *longifolium* occur.

The only moss growing submerged in ponds in Middlesex is *Fontinalis antipyretica*, recorded c.fr. by De Crespigny in one locality. It has not been found since. This species, which is well known to fruit only in still water, has not been recorded fruiting from elsewhere in the county.

(ii) *Rivers and canals.*

The various communities of mosses found in the Thames and on its banks may be classified into (i) the permanently submerged zone, (ii) the zone submerged for about half the year, (iii) the epiphytic community on willow trunks liable to submergence only during high floods.

(i) In this zone the mosses live permanently in the highly calcareous and slow-flowing river-water. They grow on the artificial banks of wooden piles or stone (usually limestone or concrete) or more rarely on loose blocks or pebbles on the river-bed in shallow water. Where the bank is more or less natural (as it is along almost the whole length of the Colne) and fringed with aquatic herbs there is scarcely any moss-flora of any kind, except a little *Fontinalis*. On the outer bank of bends in the river where the current is stronger, the moss-vegetation is also poor. The following species occur between Shepperton and Penton Hook:

Cinclidotus fontinaloides r.
Eurhynchium rusciforme o.

Fontinalis antipyretica and var. *cymbifolia* a.
Octodiceras Julianum r.

Fontinalis forms thick beds in many places in the shallower water. *Octodiceras*, which was discovered in 1926, is perhaps one of the most interesting of Middlesex mosses. It had previously been found in the Thames in Berkshire and Oxfordshire and was only discovered in Britain (in the Severn) in 1907.

¹ The allied *Ricciocarpus natans* has not yet been discovered in the county.

Mr Dixon has suggested that it may be a recent introduction which is spreading, but the facts that its geographical distribution in Europe makes it likely to be a British species and that it is very inconspicuous and grows submerged, make it on the whole more probable that it has been previously overlooked. *Octodicerias* grows from just below the normal summer water-level to not more than about 9 in. below it (as far as can be observed), attached to wood or stones. It is found in small clusters of about ten to twenty 'fronds' and is always thickly covered with epiphytic algae (diatoms, etc.).

(ii) In the zone submerged for part of the year only (usually about October to May), there are two distinct communities, viz. those on the natural clay banks and those on the artificial stone banks. The flora of these clay banks, which closely resembles that of other moist clay banks in Middlesex and has no specially aquatic characteristics, has already been dealt with (p. 291). The colonisation of dried river-mud by *Physcomitrella patens* has also been referred to (p. 293).

The artificial stone banks, made of blocks of limestone or concrete placed at an angle of about 30° to the horizontal, have a comparatively rich flora of mosses. The following is a list of species observed on them between Chertsey Bridge and Penton Hook Lock:

| | |
|---|---|
| <i>Amblystegium filicinum</i> a. | <i>Encalypta vulgaris</i> v.r. |
| <i>Barbula Nicholsoni</i> l.a. | <i>Fissidens crassipes</i> (c.fr.) l.a. |
| <i>B. sinuosa</i> l.f. | <i>Hypnum riparium</i> (c.fr.) f. |
| <i>B. vinealis</i> f. | <i>Tortula intermedia</i> o. |
| <i>Brachythecium rutabulum</i> f. | <i>T. mutica</i> r. |
| <i>Cinclidotus fontinaloides</i> (c.fr.) a. | |

In contrast to the clay banks this habitat has several species strictly confined to the river-bank. Of these, *Fissidens crassipes* is found only in the lower part of the zone (to about 1½ ft. above the summer water-level). This moss also covers stones projecting out of the water. *Cinclidotus fontinaloides* in an aquatic moss shared by this habitat and the submerged zone. Here, however, it grows shorter and more compact than in the water and it also fruits. *Barbula Nicholsoni* is confined to the Thames bank in Middlesex, where it occurs locally (e.g. below Penton Hook Lock) in great abundance. *Encalypta*, *Tortula intermedia* and *Barbula sinuosa* occur only in this habitat in Middlesex¹. They are all strongly calciphilous and may have been introduced with the stone, as so many mosses have been introduced in the rockery at Kew Gardens (12) or may perhaps be put with the ten species of flowering plants whose presence on the Middlesex banks of the Thames Trimen and Dyer (3, p. xix) thought might be due to carriage by winter floods.

(iii) A sparing moss-vegetation is found on the willows and alders of the river banks. On the alders *Leskea polycarpa* occurs sparingly and *Tortula mutica* very rarely. On the willows *Tortula mutica* occurs very constantly. It is

¹ Though there is an old record for *Encalypta* from Harefield and for *T. intermedia* from Southgate.

found typically embedded in cracks of the bark on the upper side of trunks of *Salix alba* where they lean over the water. The tufts collect so much silt that the deep cracks in the bank become completely filled up. *Leskea polycarpa* occurs on the willows almost as constantly as the *Tortula* and may form mixed tufts with it. *Orthotrichum diaphanum* and *Tortula laevipila* occur sparingly in the same habitat. These mosses all grow chiefly at a height of about four to five feet above the summer level of the river.

The canals passing through Middlesex are very dirty and their flora is extremely poor. On stones by the Grand Junction canal at Harefield the following have been observed: *Fissidens crassipes*, *Bryum pallens*, *Brachythecium populeum*, *Amblystegium filicinum* and *Lunularia cruciata*. There is no submerged flora except on the stones of sluices etc., where there is a rapid current, and here *Fissidens crassipes* and *Eurhynchium rusciforme* are found. The flora of the Lea canal is even poorer.

(iii) *Brooks.*

These are usually so dirty as to have scarcely any mosses, but *Fontinalis antipyretica* occurs in some little streams in the woods near Ruislip. Its habitat is very remarkable. In one place it grows on the roots and trunks of oaks on the margin of the brook, but raised well above it. Elsewhere it occurs in the bare pebbly bed of the stream attached to small stones which would be washed away by a moderately strong current. Where the brook crosses a clearing the *Fontinalis* has that golden colour characteristic of it in sunny streams. The brooks are very small and readily dry up, so that the *Fontinalis* spends fully half the year out of the water. In rivers and ponds this moss normally grows where it is permanently submerged.

7. VARIOUS ARTIFICIAL HABITATS.

Walls.

As there is no native stone in Middlesex all the rupestral mosses which occur on walls must be immigrants. Middlesex walls on which mosses are found are usually made of flints (especially round Harefield and South Mimms, near the chalk) or of brick. Their flora is never very abundant or very varied. Rupestral mosses are in fact, next to the arboreal, those most affected by smoke.

Tortula muralis is by far the commonest wall-moss. It penetrates London at least as far as the inner suburbs (e.g. Regent's Park) and fruits abundantly. Its abundance on any particular wall fluctuates much from year to year. In the very wet summer of 1924 it became very abundant on suburban walls and even appeared on walls where it had not been seen before. *Grimmia pulvinata*, usually a very common plant, only occurs in a few localities in Middlesex. Apart from these two species, the commonest mosses on walls

are *Camptothecium sericeum* and *Bryum caespiticiun*. The former is frequent even quite near London (e.g. wall at Hampton Court and at Ken Wood Ponds). *Grimmia apocarpa*, so characteristic a moss of limestone walls in the Midlands, is recorded from one Middlesex locality by De Crespigny (1), but has not been seen since and was probably introduced accidentally.

Mosses on walls are most abundant on the tops rather than on the vertical faces; this is probably due rather to the chances of spores settling being greater on a horizontal surface than to the smoke effect mentioned by Wheldon and Travis (18). The tufted habit of many wall-mosses is no doubt very useful to them in enabling them to collect soil, but on walls on the edge of very dusty roads, the tufts become almost spherical and apt to break loose from the stone altogether.

The following table gives the flora of a number of typical Middlesex walls.

Table V.

The Bryophytic Vegetation of Middlesex Walls.

| Species | Localities | | | | |
|--------------------------------|-----------------|-------------|--------------|------------------|----------------|
| | Brick | | | | Flint |
| | Near Mimms Hall | Canons Park | Near Ruislip | About Shepperton | Near Harefield |
| <i>Barbula fallax</i> | — | — | — | o | — |
| <i>B. rubella</i> | r. | — | — | r. | — |
| <i>B. unguiculata</i> | — | f. | r. | — | — |
| <i>B. vinealis</i> | — | — | — | o. (?) | — |
| <i>Brachythecium rutabulum</i> | a. | — | — | — | — |
| <i>Bryum argenteum</i> | — | — | — | — | o. |
| var. <i>lanatum</i> | — | — | o. | — | — |
| <i>B. caespiticiun</i> | — | a. | — | o. | — |
| <i>B. capillare</i> | — | — | — | i | r. |
| <i>Camptothecium sericeum</i> | — | o. | f. | f. | — |
| <i>Ceratodon purpureus</i> | l.a. | — | a. | a. | — |
| <i>Grimmia pulvinata</i> | r. | — | a. | v.r. | a. |
| <i>Orthotrichum diaphanum</i> | — | — | — | l.a. | — |
| <i>Tortula muralis</i> | a. | v.a. | f. | a. | f. |

To these must be added a list from a damp and deeply shaded brick-wall on the edge of Hampstead Heath, with an entirely different flora: *Eurhynchium confertum*, *E. murale*, *Hypnum riparium*.

Other mosses recorded from Middlesex walls in recent years are: *Tortula muralis* var. *aestiva*, *Funaria hygrometrica*, *Bryum inclinatum*, *Amblystegium serpens*.

The mosses of tiled roofs may be referred to here. Now-a-days little but *Ceratodon purpureus* can be found even on old roofs, but old records show *Dicranoweisia cirrata* and *Tortula ruralis* to have been common on them formerly. The latter survived on a roof near the "Spaniards," Hampstead, till 1922.

Miscellaneous habitats.

Dicranoweisia cirrata and *Tortula ruralis* formerly occurred on thatched roofs in Middlesex, but no mosses have been seen lately on the few thatched roofs left in the county.

Leptobryum pyriforme is a characteristic moss of pots in greenhouses and there are several Middlesex records of it from such situations. It is not recorded from any natural habitats in the county.

Mosses are sometimes found on rubbish-heaps and cinders, thus at Poyle a beautiful carpet of fruiting *Leptobryum pyriforme* was found, mixed with *Marchantia polymorpha* and in Colindeep Lane *Funaria hygrometrica*, *Bryum atropurpureum* and *B. argenteum* were found on cinders on waste ground in 1923. *Funaria* occurred abundantly on asbestos rubbish at Harefield in 1925.

Very few mosses occur in central London. *Bryum argenteum* is very common on stones by canals, cinders, walls, cracks in pavements, etc. and occurs throughout London (e.g. on a very smoky piece of ground by the L.M.S. railway line at Euston and with *Ceratodon* on the site of demolished buildings in Holborn in 1921).

CONCLUSIONS.

While more work will need to be done in other districts before it will be possible to come to any general conclusions on the ecology of bryophytes, it is perhaps worth noting the general effects of the peculiar local conditions in Middlesex, i.e. the huge proportion of its surface which is built over.

A total of about 227 species of bryophytes have been recorded from Middlesex and some 154 have been refound during the period 1920-27. The loss has therefore been about 32 per cent.—not, perhaps, as large as might be expected. This may be compared with 24 per cent. loss in a district near Liverpool (7) and with Loeske's results for Berlin, given in a recent paper (9). In that district, he says, the moss-flora has really changed in the last decades, but there has been no actual impoverishment in number of species, though some of the choicer mosses have to be looked for further from the town than formerly. That the effect of London's growth on the Middlesex moss-flora has really been profound is shown by the facts that 51 per cent. of the species are found only in three localities or less and nearly 26 per cent. are found in one locality only, though these high percentages are partly due to the small number of places where certain types of soil (e.g. chalk) occur.

The sensitiveness of arboreal mosses to smoke has been mentioned on p. 274.

The value of mosses as indicators of vanished plant associations is shown by the facts given on the vegetation of Middlesex heaths.

The facts observed about the variations in the abundance of the mosses in Hampstead Bog, suggest that one of the effects of urbanisation may be to intensify the fluctuations which seem to occur normally in moss-vegetation.

ACKNOWLEDGMENTS.

The author wishes to express his thanks to Mr R. D'O. Good and Dr E. J. Salisbury for their kind help and encouragement, without which this paper would never have been written. He is also indebted to the Referees of the British Bryological Society for many identifications of mosses, especially to Mr W. R. Sherrin who has also generously given much help in other ways.

SUMMARY.

1. The bryophytic vegetation of an area in south-eastern England is described from the ecological and floristic points of view.

2. The general features of the district are described. The most important local characteristic is the high degree of urbanisation. The effects of this on the moss-vegetation are emphasised.

3. The moss-vegetation of oak-hornbeam woods (*Quercetum sessiliflorae* with *Q. Robur* and *Carpinus Betulus*) is described, also that of birchwood and scrub derived from oakwood. The woodland moss-vegetation is analysed into four strata (tree-trunks, tree-bases and stumps, wood-floor and woodland banks) and the characteristic types of bryophytes in each are indicated. The bryophytic vegetation of birchwoods shows some resemblance to that of heaths.

4. The moss-vegetation of hedges on chalk and on grassland clay soils is described. The mosses of hedges are essentially a concentrated essence of those of woodland on the same type of soil, though most of the species of the wood-floor are lacking. The flora of the chalk and clay hedges has much in common.

5. The moss-vegetation of some relict heathland is described. The changes in the cryptogamic vegetation following the conversion of *Callunetum* into grass-heath are discussed. The very characteristic moss and lichen vegetation of the *Callunetum* has a remarkable power of persistence in small relict islands of *Calluna*. The flora of some bogs is described and found to include some bryophytes which are normally strictly calcicolous. The vegetation of one of the bogs shows extraordinary fluctuations.

6. Bryophytes occur only sporadically on grassland on clay and alluvium owing to the competition of the higher plants.

7. A number of purely cryptogamic communities are described and classified into (i) perennial, (ii) winter ephemeral, (iii) summer ephemeral.

8. Tables are given for each habitat of the species (with frequencies) from a number of specimen localities.

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THE ECOLOGY OF DIVIS

By M. P. H. KERTLAND.

(With three Figures in the Text.)

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INTRODUCTION.

The first ecological study of mountain vegetation in the British Isles was published by Robert Smith in Scotland in 1900 (9). This was followed by extensive investigations by W. G. Smith (8), Moss (4), Rankin (8), Lewis (3) and Adamson (1), of the vegetation groups of the Pennines, and the work of Crampton and Macgregor (2) on Ben Armine. So far the only study of this kind in Ireland is that of Pethybridge and Praeger (7) on the moorland vegetation of Wicklow. The present paper may be regarded as a small extension of this type of study to a limited area of the northern mountain region in Ireland.

The investigation of peat, its characteristic plants, formation and stratification dates much further back. Clements (28) in his chronological summary of ecological papers up to 1915 quotes King (1685) *On the Bogs and Loughs of Ireland*, as one of the earliest of these accounts. The most recent work on peat in Britain has been chiefly geological and historical, that of Lewis (20),

Erdtman (11-14), Forbes (17), Pearsall (18), C. Reid (24) and E. M. Reid (30), on the evidence of past flora in the peat strata, Lewis and Erdtman holding that climatic changes have been the chief factors in the alternating flora of the layers, and Pearsall that this alternation is not necessarily influenced by climate but is due to the general trend of succession on poor soil.

Weber, Erdtman and E. M. Reid consider that statistics of the different kinds of pollen grains preserved in the peat at different levels are the most satisfactory guide to the consecutive history of woodland floras since post-glacial times. Erdtman has investigated numerous peat deposits including some Irish beds, and has compiled a bibliography (15) of the literature dealing with the pollen statistics of peat before 1927.

METHODS OF WORK.

Mapping. First, the most marked vegetation groups were roughly filled in to a 6-in. Ordnance Survey map (scale 1 : 10560). As there are in such maps no contours drawn and few land marks over 1000 ft. (305 m.), the boundaries of the associations were difficult to fix, especially in broad transition regions, where the dominance of any one species is indefinite.

An enlargement to a scale of 12 in. to the mile was made from a 6-in. map, and features acting as landmarks and boundaries of vegetation communities were filled in from observations. To make a detailed survey the map was divided into 2-in. squares; equivalent to the 1-in. squares of the 6-in. Ordnance map, each square being equal to an area of moorland, 293 yds. (267.9 m.) square. To facilitate mapping, each square was re-divided into three strips, each equivalent to 98 yds. (89.6 m.) in width. In practice this square was mapped in tenths, two surveyors being required, one at each end of a cord 29.3 yds. (26.8 m.) long, each surveyor walking, as far as possible, in parallel lines and mapping in any outstanding features, especially at the 98 yds. marks, which were counted as 100 paces apart.

On the gentler slopes, where a whole square could be under observation at once, such a laborious method was not always necessary, and the landmarks and boundaries could be plotted in from measurements made from the sides of the squares already surveyed.

Corrections as to boundaries of associations were made on the 6-in. map from the data mapped in the large scale map.

General. Geological and climatic data were obtained from local records. No detailed soil analyses was made, though rough estimates of comparative soil acidity were made by the use of Wherry's table for the determination of hydrogen-ion concentration (31).

The floristic lists were made from personal observations. They are probably not exhaustive, as the greater part of the work was done in the winter months, when it was impossible not to overlook many perennial species

and identification of grasses was difficult. This problem of "seasonal aspect" was most pronounced in the grassland areas.

The frequency symbols used are those recommended by Tansley (36): d. = dominant; a. = abundant; f. = frequent; o. = occasional; r. = rare. The letter "l." is prefixed to the symbol when the dominance, abundance or frequency is only local, and the letter "v." is prefixed when the abundance or rarity is striking, thus: l.a. = locally abundant, and v.a. = very abundant.

Similar symbols noted for the square sub-sections of the map have been translated into the Braun-Blanquet and Pavillard (32) figure scale of frequency in a Frequency Table (not included here).

Fossil pollen. On the summit plateau the peat at various depths was examined for evidence of the composition of past flora. Some semi-buried wood was found which proved to be *Crataegus oxyacantha* (agg.). Samples of peat were taken from a vertical bore in a peat hag and prepared for microscopical examination by a modification of the methods used by Erdtman (11) and E. M. Reid (30). A portion of each sample was digested with 10 per cent. caustic potash in a test-tube for approximately 6 hours. It was then poured through a porcelain filter to separate off any plant remains for identification. The finer material was collected in a centrifuge and a small portion of the precipitate placed on a slide with a cover-glass so that the pollen grains might be identified and counted. As far as possible the treatment and amount of material from each sample were made uniform with a view to comparing pollen frequencies.

FACTORS.

1. *Topographical.* Divis is the highest of the group of mountains which dominate the head of the Belfast Lough. It lies in the latitude of 54° 37' N. and the longitude of 6° 1' W., about four miles (7 km.) north-west of Belfast, from whence the summit is easily accessible via Ballygomartin or Ligoniel, the latter route passing over Wolfhill.

The area covered in this paper consists of about 1½ square miles (5·8 sq. km.) of enclosed moorland, including the summits of Divis (1575 ft.) (480 m.) and Wolfhill (1215 ft.) (370 m.), which form the south-eastern boundary of the Antrim plateau. The general level of the moor is about 1100 ft. (335 m.), a gently undulating plateau falling steeply down to the 600 ft. (183 m.) level on the east, and sloping more gradually on the other three sides. This edge of the plateau presents a line that is slightly higher than the surrounding moorland, and acts as a watershed between the Lagan and the Lough Neagh valleys. The streams are not large nor important, but even the smallest has a rapid flow. The Clady drains to the west, joining the Six Mile Water near Crumlin, the Big River rises in Johnston's Green and joins the Colin River to the south, and the Forth drains the dip between Divis and Wolfhill and is the most rapid, flowing in a series of falls into the Ballygomartin district

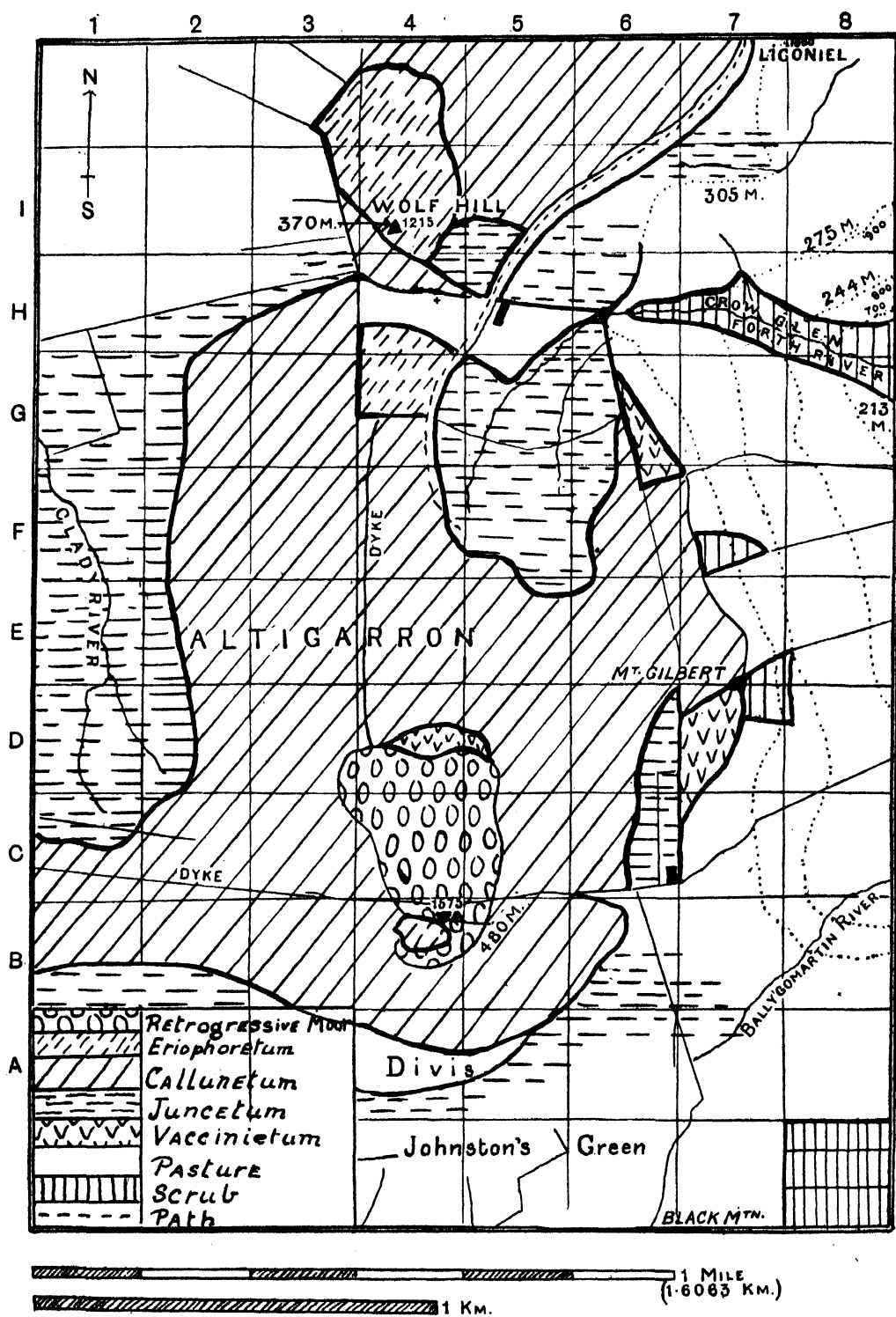


FIG. 1. Vegetation sketch map of the Divis area.

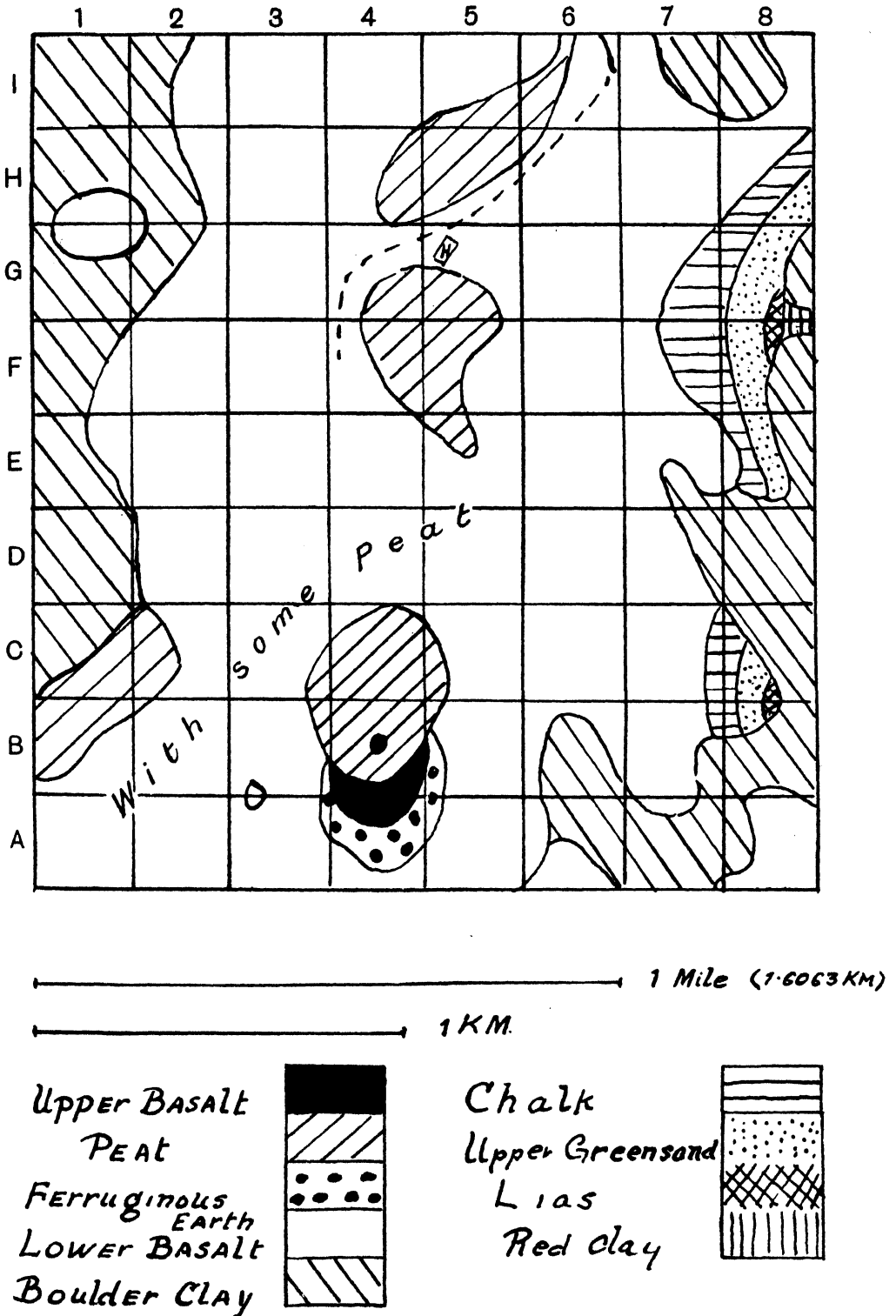


FIG. 2. Drift map of the Divis area.

through Crow Glen. Another small stream (the Ballygomartin River) rises near the keeper's cottage to the south-east of Divis, and flows in the same direction as the Forth.

The mountain is divided into the districts of Altigarron and Divis, by a boundary dyke running east and west near the summit of Divis; a second dyke at right angles to the first runs to Wolfhill.

2. *Geological*. The plateau of which this district forms a part is of Tertiary basalt overlying cretaceous limestone, and is covered with "Wide sheets of flat bog or deposits of glacial gravels and clays." There is evidence of glacial deposit on Divis.

The underlying limestone is not exposed in the parts under discussion. Thus a non-calcareous type of soil predominates, and a large area is definitely acidic with a low mineral content and a large amount of humus.

The sketch (Fig. 2, p. 305) from a drift map is interesting to compare with the vegetation map (Fig. 1, p. 304).

The greatest area is of lower basalt with a layer of peat; it will be seen that this is almost equivalent to the extent of the dominance of *Calluna* and its transitional associations. There is even more striking correlation between the areas occupied by *Juncetum* and those covered by boulder-clay in the Clady, Big and Ballygomartin valleys and the wet farm lands at Wolfhill.

Deep peat is recorded on the summit plateau, which, on the vegetation map, is indicated as retrogressive moor under partial dominance of *Eriophorum angustifolium*. The peat area on Wolfhill lies somewhat in a hollow within the *Calluna* association and is characterised by an abundance of *Sphagnum*, *Scirpus caespitosus*, *Eriophorum vaginatum* and *Carex* spp. *Sphagnum* is also very abundant in the peat of the three waterlogged hollows where the Clady, Forth and Big rivers rise.

The margin of grass on the eastern slopes coincides with the outcrop of chalk indicated on the geological map.

3. *Climatic*. Owing to its inaccessibility, it was not possible to make weather records for Divis, so the mean for the district has been taken as a rough indication of climatic conditions.

The following figures are taken from the British Meteorological Report for 1923:

| | Height (feet) | Rainfall (inches) | Days* |
|-----------------------|---------------|-------------------|-------|
| Ballymena | 150 (46 m.) | 39.53 (1004 mm.) | 278 |
| Stoneyford, Belfast | 437 (138 m.) | 49.46 (1256 mm.) | 223 |
| Lisburn | 208 (63 m.) | 50.46 (1282 mm.) | 268 |
| University, Belfast | 62 (19 m.) | 45.42 (1154 mm.) | 244 |
| Oldpark, Belfast | 203 (62 m.) | 48.08 (1221 mm.) | 249 |
| Dorisland, Carrick | 250 (76 m.) | 41.19 (1046 mm.) | 249 |
| Woodburn, Carrick | 640 (195 m.) | 50.41 (1280 mm.) | 261 |
| N. Woodburn, Carrick | 737 (225 m.) | 50.21 (1275 mm.) | 262 |
| Copeland, Carrick | 424 (129 m.) | 37.86 (962 mm.) | 240 |
| Lough Mourne, Carrick | 596 (182 m.) | 44.36 (1127 mm.) | 241 |

* Number of days on which 0.01 in. (0.3 mm) or more fell.

The mean rainfall in 1923 for the district was thus 45·7 in. (1160 mm.).

The following details for 1923 were recorded at Queen's University, Belfast:

| | Rainfall (inches) | Rain-days (on which 0·01 in. (0·3 mm.) or more fell) | Temperatures ° F. | |
|-----------|----------------------|--|-------------------|-----------------|
| | | | Abs. max. | Abs. min. |
| January | 4·13 (105 mm.) | 26 | 52 (11° C.) | 31 (– 0·5° C.) |
| February | 6·88 (175 mm.) | 27 | 52 (11° C.) | 29 (– 1·6° C.) |
| March | 2·28 (58 mm.) | 15 | 57 (14° C.) | 30 (– 1° C.) |
| April | 3·68 (93·5 mm.) | 19 | 63 (17·25° C.) | 34 (1° C.) |
| May | 1·35 (34 mm.) | 21 | 67 (19·5° C.) | 36 (2·25° C.) |
| June | 0·72 (18 mm.) | 16 | 71 (21·75° C.) | 48 (9° C.) |
| July | 2·89 (73 mm.) | 21 | 83 (28·25° C.) | 53 (11·75° C.) |
| August | 6·6 (168 mm.) | 21 | 75 (24° C.) | 41 (5° C.) |
| September | 3·78 (96 mm.) | 23 | 70 (21° C.) | 38 (3·25° C.) |
| October | 4·27 (108 mm.) | 29 | 64 (17·75° C.) | 30 (– 1° C.) |
| November | 4·29 (109 mm.) | 29 | 55 (12·75° C.) | 27 (– 2·75° C.) |
| December | 4·55 (110 mm.) | 27 | 54 (12·25° C.) | 29 (– 1·6° C.) |
| | | 274 | | |

The maximum temperature recorded was 83·6° F. (28·6° C.) on July 6th, and the minimum 27·6° F. (– 2·5° C.) recorded for November 21st. Fogs are most frequent in October, November and December; and frosts most frequent from November to March, when the summit is often snow covered.

Climatic conditions being more or less uniform over a large area, it is sufficient to point out that the elevation and exposure on Divis would increase the amount of rainfall, and lower the temperature.

The prevalent wind is from the south-west, a wet wind with occasional strong northerly and easterly variations. The eastern slope is the most sheltered, and the effect of climatic agencies is most marked on the summit plateau.

4. *Edaphic*. The bulk of the soil is acid peat, frequently saturated and insufficiently drained. There is little variation in the soil acidity, but it is less marked on the eastern slopes, and around the Forth river. The water content is the chief determining factor of the vegetation areas. The amount of water present is partly governed by the subsoil—the impermeable boulder-clay hindering drainage—and partly by the geographical configuration, which leads to accumulation of moisture in the dips to north, west and south of Divis and increased drainage on its eastern slopes.

| | pH value |
|-----------------------------|----------|
| Summit peat (Divis) | 4·5–5 |
| Callunetum (Mt. Gilbert) | 4·5–5 |
| Callunetum (Wolfhill) | 4·5–6 |
| Scirpetum (Wolfhill) | 4·5–5 |
| Juncetum (Johnston's Green) | 4·5–5 |
| Nardetum (Wolfhill) | 6 –7 |

5. *Biotic*. Man, with his ditching, ploughing and burning, is the dominant biotic factor. The two former alter the normal successional course by increasing drainage and removing the vegetation. The latter has probably little

more than temporary effect. Man also indirectly influences the vegetation by shooting rabbits, and grazing his sheep and cattle on various areas. This latter factor is probably of little importance here except in marginal areas. Plant competition determines the dominance of *Calluna vulgaris* and is probably an important though not so obvious a factor in other associations.

ZONATION OF VEGETATION.

The vegetation of the area lies within the Formation of Acidic Peat Moors, and is chiefly under the dominance of *Calluna vulgaris* and *Eriophorum angustifolium* with numerous sub-associations and facies due to variation in drainage and elevation.

The zonation on the eastern slope is obvious and typical. Societies of *Juncus communis* give place to a broad slope of dry grass pasture with traces of degenerating scrub. This in turn leads to a transition association of mixed bilberry and heather, where the flora is rich in species, some typical of woodland, e.g. *Luzula sylvatica*, *Scilla non-scripta*, *Digitalis purpurea*. Beyond again, *Calluna vulgaris* is dominant, giving place on the summit to *Eriophorum* which dominates the wetter hollows while *Vaccinium myrtillus* occupies the peat hags. This zonation is fairly general, with local variations, as around springs, where *Juncus communis* dominates the better aerated soil, or in stagnant depressions, where *Sphagnum* and *Eriophorum* thrive. The transition regions are broad and show co-dominance of bordering associations.

THE SUMMIT PLATEAU.

The summit plateau is typical of the retrogressive moorland community. Once entirely peat clad, it has been channelled and scoured by the successive action of frost, wind and water until only isolated peat hags remain. These are being gradually worn away by the cutting back of the drainage channels, and their complete removal is only a matter of time.

The substratum of the summit slopes slightly upwards from east to west. To the west, the peat has an average depth of about 2 ft. (610 mm.), but extensive areas have been completely denuded of peat, leaving an area of stones and boulders limited at the edges by low peat hags. *Nardus stricta*, *Juncus squarrosus* and *Calluna vulgaris* occupy any pockets of peat remaining between the stones, and *Rhacomitrium lanuginosum* and lichens have to some extent colonised the bared rock. On the east *Veronica officinalis* has spread on to some patches of fine gravel.

To the east of the plateau, the deeper peat (4 ft.) (1.2 m.), marks the slope of the substratum. The channels are broad and deep, but only in the deepest channels is the rock exposed, the majority of the channel beds being of loose peat devoid of vegetation, except occasional plants of *Rumex acetosella* (dwarf), which is the last species to be washed out of the unstable soil.

The peat hags vary in size from 10 sq. ft. (0.9 sq. m.) to 25 sq. yds. (20 sq. m.), and all have typical overhanging edges due to the erosion of the peat support; this in the smaller hags leads to the general contour being definitely convex and the top layer of soil being generally dry, as any excess of water quickly drains away. The larger hags have an undulating surface, the hollows are filled with *Eriophorum* and *Sphagnum*, while the dry edges show a greater abundance of *Vaccinium* and *Calluna*. To a general view, *Calluna* is dominant on the peat hags, but there are more shoots of *Eriophorum* and it is multiplying rapidly while *Calluna* seedlings are rare. Around pools and in wet hollows *Eriophorum angustifolium* is completely dominant.

The above-mentioned plants are the only inhabitants of this area, excepting the species present in the close turf of the mound surrounding the cairn. Here we find *Luzula campestris*, *Poa annua*, *Festuca ovina*, *Carex caespitosus*, *Galium saxatile* and *Potentilla erecta*, with *Hylocomium squarrosum* in abundance.

There are two pools in the vicinity of the cairn which fairly constantly contain water to the depth of about 4 in. (101.6 mm.), depending on the rainfall. The soil deposit is black and structureless, with occasional shoot bases of *Eriophorum angustifolium*; *Cylindrocapsa* and Diatoms are found in abundance. Cotton-grass is the only invader, and is encroaching rapidly. It is dominant in the marginal vegetation and, judging by the plant remains in the upper layers of the peat hags, the whole summit was at one time under its dominance.

Juncus communis is not abundant in this area, so a small patch which occurs near the mound to the south-east of the summit cairn, is conspicuous: here *Polytrichum commune* also flourishes. An isolated patch of *Luzula sylvatica* is found on the southern slope of the summit, and may be an indication of former woodland vegetation, since a stunted specimen of *Sorbus aucuparia* has been found near by.

Species found on the summit plateau:

| FLOWERING PLANTS. | | MOSSES AND LICHENS. | |
|---------------------------------|------|--------------------------------|------|
| <i>Calluna vulgaris</i> | a. | <i>Cladonia pyxidata</i> | o. |
| <i>Empetrum nigrum</i> | l. | <i>Hypnum cupressiforme</i> | o. |
| <i>Erica cinerea</i> | f. | <i>H. var. ericetorum</i> | a. |
| <i>Eriophorum angustifolium</i> | v.a. | <i>Lecanora</i> spp. | f. |
| <i>E. vaginatum</i> | f. | <i>Lecidea</i> | d. |
| <i>Juncus communis</i> | l. | <i>Polytrichum commune</i> | l. |
| <i>J. squarrosus</i> | f. | <i>Racomitrium lanuginosum</i> | a. |
| <i>Nardus stricta</i> | o. | <i>Sphagnum</i> spp. | v.a. |
| <i>Rumex acetosella</i> | f. | | |
| <i>Scirpus caespitosus</i> | f. | | |
| <i>Vaccinium myrtillus</i> | a. | | |
| <i>Veronica officinalis</i> | l. | | |

Additional species from the turf of the summit cairn:

| | |
|------------------------------|--------------------------|
| <i>Carex caespitosus</i> | <i>Luzula campestris</i> |
| <i>Festuca ovina</i> | <i>Poa annua</i> |
| <i>Galium saxatile</i> | <i>Potentilla erecta</i> |
| <i>Hylocomium squarrosum</i> | |

ERIPHORETUM.

There are no extensive areas of pure Eriophoretum, but *Eriophorum angustifolium* is abundant throughout the mountain area and *Eriophorum vaginatum* is frequent on Wolfhill. *Eriophorum angustifolium* becomes dominant in wetter hollows around the retrogressive moor area where the drainage is retarded, as on the terrace to the south-west of the summit, on parts of Johnston's Green and on the northern aspect of Wolfhill. In the latter area *Scirpus caespitosus* is largely co-dominant.

The chief species in these Eriophoreta are:

| | | | |
|---------------------------------|------|-----------------------------|------|
| <i>Calluna vulgaris</i> | o. | <i>Eriophorum vaginatum</i> | l.a. |
| <i>Erica cinerea</i> | o. | <i>Polytrichum commune</i> | a. |
| <i>E. tetralix</i> | o. | <i>Scirpus caespitosus</i> | o. |
| <i>Eriophorum angustifolium</i> | l.a. | <i>Sphagnum</i> spp. | a. |

CALLUNETUM.

This is the chief association on Divis, extending over the whole area from 1100 ft. (335 m.) up.

On deep peat (2-4 ft.) (0.610-1.2 m.) the association is floristically poor, owing to the luxuriant growth of the dominant *Calluna vulgaris*, and the associated *Erica cinerea*, which present a uniform covering of closely interlocked bushes from 1 to 2 ft. (0.3-0.6 m.) in height, so that subordinate species are deprived of light and only survive in local patches or in an etiolated condition. This association is typically dominant in the areas immediately surrounding the retrogressive moor, extending down to approximately 1200 ft. (365.7 m.).

This Callunetum is a closed association on peat, averaging about 2 ft. (0.6 m.) in depth. The unbroken surface layer is composed of heather tops closely covered with small evergreen leaves; the next layer of woody stems profusely branched, either bare or still retaining a few dying leaves, and the floor is covered by numerous trailing stems buried in thick layers of fallen leaves. The upper surface provides a thick canopy, so that the only constant associates are plants which can compete by outgrowing or overgrowing the heather, or can survive the shade. *Erica cinerea* is abundant; having similar structural modifications to *Calluna*, it is able to keep its footing. *Eriophorum angustifolium* is usually very abundant, it shoots up higher than the general heather level and so is not seriously handicapped by the shade: being deeper rooted, the factor of root competition does not occur.

Vaccinium myrtillus, *Potentilla erecta* and *Galium saxatile* are frequent but not conspicuous. They are usually much etiolated except where there is a break in the general surface of the Callunetum. In hollows where water has collected, near springs, or where ditches have been dug, *Juncus* societies appear and are very conspicuous. *Scirpus caespitosus* is also fairly frequent, and occasionally dominant in areas where the heather has been burnt and the

soil is not favourable for *Vaccinium myrtillus*. Such a patch is conspicuous to the west of the summit (square C 3).

Where dykes (made banks) or tracks traverse the Callunetum, there is a conspicuous change in the vegetation. The dykes are usually dominated by *Vaccinium myrtillus* and various "turf-grasses," such as *Poa annua* and *Festuca ovina*, while *Nardus stricta* is typical of tracks; indeed, its clumps of fine leaves, bright green in summer and white in winter, are a trustworthy guide to the most suitable tracks by which the ascent of Divis may be made.

Lycopodium selago is found in abundance in patches to the west and north of the summit. *Pyrus aucuparia* (dwarf) is very rare in the heather moor, only one plant has been found to the south, and one to the north of the summit plateau. *Blechnum spicant* and *Dryopteris* spp. (undetermined) are occasionally found in sheltered positions.

Mosses and lichens are fairly abundant. *Hypnum cupressiforme* var. *ericetorum* seems best able to withstand the dense shade of the Callunetum, while the common variety with *Breutelia arcuata* and *Racomitrium* spp. are fairly frequent in less shaded patches. *Sphagnum* is abundant and dominates all other mosses in hollows where water has collected; it may compete with the heather itself to the latter's ultimate destruction, since the moss speedily grows through and overtops the heather, which is hampered by reduced root absorption from the waterlogged soil.

Another interesting facies of the heather association is seen to the west of the north-south Dyke, where *Racomitrium* becomes subdominant quite extensive patches clothing the sides of the hummocks with their thick mats of hairy leaves. This part of the moor shows much more of a hummock formation and corresponds on a small scale to the moss-lichen moor of W. G. Smith (8).

Cladonias are the dominant lichens, but *Lecanora* is abundant on all rocks. *Cladonia rangiferina* is conspicuous in the above-mentioned *Racomitrium* area. *Cladonia pyxidata*, *C. coccifera* and *C. macilenta* have all been found fairly frequently.

As the mountain is preserved land, there are patches of heather burned from year to year, to make room for new growth of heather seedlings. The heather burns rapidly owing to its low water content, and large areas of moor may be left bare save for the charred stems of *Calluna*. Regeneration by seedlings is often very slow. Here there is an opportunity for the spread of any subordinate species with more facile means of regeneration. *Vaccinium*, *Eriophorum* and *Scirpus* are less affected by the fire, being less easily burned. Able as they are to send up adventitious shoots, they quickly attain full growth while the *Calluna* is still only in the seedling stage. In many burned areas, *Scirpus* has become dominant with *Eriophorum* associated, and there is as yet little sign of the recovery of *Calluna*, though the burning took place about two years ago. On the north slope of the summit there is an area now

dominated by *Vaccinium myrtillus*. A large extent in the north-east of the Callunetum area has been burnt this year.

Rabbits are fairly abundant and there is usually a close-cropped circle of turf surrounding the burrows; but rabbit attack does not alter the vegetation to any large extent, though in some cases these animals are responsible for undermining dykes, which, on falling in, expose bare areas for colonisation or denudation.

The following is a list of species found in the Callunetum areas on Divis:

| VASCULAR PLANTS. | | | |
|---------------------------------|------|----------------------------------|----|
| <i>Alchemilla vulgaris</i> | o. | <i>Potentilla erecta</i> | f. |
| (<i>Blechnum spicant</i>) | o. | <i>Rumex acetosella</i> | o. |
| <i>Calluna vulgaris</i> | dom. | <i>Scirpus caespitosus</i> | f. |
| <i>Carex flacca</i> | o. | <i>Sorbus aucuparia</i> | r. |
| <i>Crataegus monogyna</i> | l. | <i>Vaccinium myrtillus</i> | f. |
| (<i>Dryopteris dilatata</i>) | r. | | |
| <i>Erica cinerea</i> | a. | MOSSES. | |
| <i>E. tetralix</i> | o. | <i>Breutelia arcuata</i> | f. |
| <i>Eriophorum angustifolium</i> | v.a. | <i>Hypnum cupressiforme</i> | f. |
| <i>E. vaginatum</i> | o. | var. <i>ericetorum</i> | a. |
| <i>Festuca ovina</i> | o. | <i>Polytrichum commune</i> | f. |
| <i>Galium saxatile</i> | f. | <i>Ptychomitrium polyphyllum</i> | f. |
| <i>Hieracium pilosella</i> | o. | <i>Rhacomitrium fasciculare</i> | f. |
| <i>Juncus communis</i> | l.a. | <i>R. lanuginosum</i> | a. |
| <i>Luzula campestris</i> | o. | <i>Sphagnum</i> spp. | a. |
| <i>L. sylvatica</i> | r. | | |
| (<i>Lycopodium selago</i>) | l. | LICHENS. | |
| <i>Nardus stricta</i> | o. | <i>Cladonia coccifera</i> | o. |
| <i>Orchis mascula</i> | r. | <i>C. macilenta</i> | o. |
| <i>Pedicularis sylvatica</i> | o. | <i>C. rangiferina</i> | f. |
| <i>Poa annua</i> | o. | <i>C. pyxidata</i> | f. |
| | | <i>Lecanora</i> spp. | f. |

On shallower peat, marginal to the pure Callunetum, the full competitive power of the heather is not developed, and there is an abundance of associated species transitional to the communities of Juncetum, Vaccinietum, Nardetum and scrub.

This mixed association of *Calluna* is typical of the margin of the Wolfhill area, which is covered with wet shallow peat. Here vegetation is not fully developed, evidently owing to a slow recovery from firing, and there are numerous bare patches, especially towards the summit. *Calluna vulgaris* in an immature stage is abundant over the whole area, except on the badly drained northern slope where *Eriophorum* and *Scirpus* are co-dominant with abundant *Sphagnum* and *Polytrichum commune*. In comparison with the previously described pure *Callunetum vulgaris* this mixed community is floristically rich, as is to be expected in an area where the full competitive power of *Calluna* is not developed.

The flora includes:

| VASCULAR PLANTS. | | | |
|-------------------------------|----|--------------------------|------|
| <i>Achillea ptarmica</i> | r. | <i>Calluna vulgaris</i> | a. |
| <i>Agrostis vulgaris</i> | f. | <i>Carex caespitosus</i> | f. |
| <i>Alchemilla vulgaris</i> | f. | <i>C. flacca</i> | l.a. |
| <i>Anthoxanthum odoratum</i> | a. | <i>C. flava</i> | f. |
| (<i>Blechnum spicant</i>) | l. | <i>Centaurea nigra</i> | o. |
| (<i>Botrychium lunaria</i>) | r. | <i>Cirsium palustre</i> | o. |

VASCULAR PLANTS (contd).

| | |
|---------------------------------|------|
| <i>Crataegus monogyna</i> | r. |
| <i>Deschampsia flexuosa</i> | f. |
| <i>Erica cinerea</i> | a. |
| <i>E. tetralix</i> | f. |
| <i>Eriophorum angustifolium</i> | l.a. |
| <i>E. vaginatum</i> | f. |
| <i>Festuca ovina</i> | f. |
| <i>Fragaria vesca</i> | o. |
| <i>Galium saxatile</i> | a. |
| <i>G. verum</i> | o. |
| <i>Hieracium pilosella</i> | a. |
| <i>Hypericum pulchrum</i> | o. |
| <i>Juncus acutiflorus</i> | f. |
| <i>J. communis</i> | l.a. |
| <i>Lathyrus montanus</i> | r. |
| <i>Listera cordata</i> | v.r. |
| <i>Lotus corniculatus</i> | o. |
| <i>Luzula campestris</i> | f. |
| <i>L. sylvatica</i> | o. |
| <i>Nardus stricta</i> | a. |
| <i>Narthecium ossifragum</i> | f. |
| <i>Pedicularis sylvatica</i> | f. |
| <i>Plantago lanceolatus</i> | f. |
| <i>Polygala vulgaris</i> | o. |
| <i>Potentilla erecta</i> | a. |
| <i>Ranunculus acris</i> | a. |
| <i>Rumex acetosella</i> | f. |
| <i>Salix repens</i> | f. |
| <i>Scabiosa succisa</i> | f. |
| <i>Scirpus caespitosus</i> | l.a. |
| <i>Senecio jacobea</i> | o.l. |
| <i>Ulex europaeus</i> | l. |
| <i>Vaccinium myrtillus</i> | a. |
| <i>Veronica officinalis</i> | o. |
| <i>V. serpyllifolia</i> | o. |
| <i>Viola canina</i> | l. |

MOSSES.

| | |
|----------------------------------|--------|
| <i>Andreaea petrophila</i> | v.r. |
| <i>Brachythecium purum</i> | f. |
| <i>Bryum capillare</i> | a. |
| <i>Breutelia arcuata</i> | o. |
| <i>Campylopus pyriformis</i> | l.a. |
| <i>Dicranum majus</i> | a. |
| <i>Dicranella heteromalla</i> | o. |
| <i>Grimmia apocarpa</i> | o. |
| <i>G. pulvinata</i> | o. |
| <i>Hylocomium squarrosum</i> | l. |
| <i>Hypnum cupressiforme</i> | a. |
| <i>H. schreberi</i> | a. |
| <i>Oligotrichum hercynium</i> | f. |
| <i>Polytrichum aloides</i> | l.a. |
| <i>P. commune</i> | l.v.a. |
| <i>P. piliferum</i> | f.l. |
| <i>Ptychomitrium polyphillum</i> | a. |
| <i>Rhacomitrium aciculare</i> | f. |
| <i>R. fasciculare</i> | f. |
| <i>R. lanuginosum</i> | l.a. |
| <i>R. protensum</i> | o. |
| <i>Sphagnum</i> spp. | v.a. |
| <i>Thuidium tamariscinum</i> | o. |

LIVERWORTS.

| | |
|------------------------------|----|
| <i>Alicularia scalaris</i> | f. |
| <i>Diplophyllum albicans</i> | f. |
| <i>Pellia epiphylla</i> | l. |

LICHENS.

| | |
|---------------------------|----|
| <i>Cladonia coccifera</i> | o. |
| <i>C. macilenta</i> | o. |
| <i>C. pyxidata</i> | f. |
| <i>C. rangiferina</i> | a. |
| <i>C. squamosa</i> | l. |
| <i>Iccanora</i> spp. | f. |
| <i>Peltigera canina</i> | l. |

JUNCETUM.

This marks a transition from peat to wet neutral soils. In the region of springs and where the numerous tributaries of the Clady, Big and Forth rivers rise, *Juncus communis* and *Juncus acutiflorus* are dominant; sometimes as pure societies within or bordering on the Callunetum, sometimes as a mixed community, transitional to wet grasslands. The representative flora of the upper tributaries of the Forth river includes the following species:

FLOWERING PLANTS.

| | |
|------------------------------|----|
| <i>Achillea ptarmica</i> | o. |
| <i>Agrostis alba</i> | f. |
| <i>A. vulgaris</i> | a. |
| <i>Ajuga reptans</i> | o. |
| <i>Alchemilla vulgaris</i> | o. |
| <i>Alopecurus pratensis</i> | o. |
| <i>Anthoxanthum odoratum</i> | f. |
| <i>Bromus mollis</i> | r. |
| <i>Caltha palustris</i> | o. |
| <i>Carex flacca</i> | o. |
| <i>Cirsium palustre</i> | f. |
| <i>Festuca ovina</i> | o. |
| <i>Holcus lanatus</i> | o. |
| <i>Lychnis flos-cuculi</i> | o. |
| <i>Mentha aquatica</i> | o. |

| | |
|----------------------------|----|
| <i>Pinguicula vulgaris</i> | o. |
| <i>Plantago lanceolata</i> | o. |
| <i>Poa pratensis</i> | o. |
| <i>Ranunculus acris</i> | f. |
| <i>R. flammula</i> | a. |
| <i>Scabiosa succisa</i> | f. |
| <i>Ulmaria palustris</i> | o. |

MOSSES.

| | |
|-------------------------------|----|
| <i>Brachythecium rivulare</i> | o. |
| <i>Bryum pallens</i> | a. |
| <i>Hypnum revolvens</i> | o. |
| <i>Philonotis fontana</i> | f. |
| <i>Polytrichum commune</i> | o. |
| <i>Sphagnum</i> spp. | f. |

Bryum pallens is typical of rocks in the bed of the stream.

The wet hollow of Johnston's Green has been to some extent artificially drained by numerous channels cut in the peat. The undrained portions are still under the dominance of *Eriophorum angustifolium*, while near the channels there is an abundance of rushes and grasses.

In parts of the areas before mentioned the rushes are cut and removed in the autumn, a procedure which keeps their growth in check. Where they are not disturbed and die down *in situ*, they cloak the substratum, and prevent any successful invasion by wet grassland species. This is well seen in the upper eastern tributaries of the Forth river.

VACCINIETUM.

The bilberry is typical of the light sandy peat of the steep well-drained eastern slopes of Mount Gilbert, and of the banks bordering tracks traversing the mountain. *Vaccinium myrtillus*, being deciduous, is very inconspicuous during the winter months, but in these areas it is obviously dominant from late April to October, as it is the first of the moorland plants to send out new shoots, and its red-tinged leaves show up against the dusky brown of the heather. This dominance is very much obscured during the winter months and, where the Vaccinietum merges with hill pasture, grasses seem entirely dominant until the summer.

The zone of Vaccinietum, lying, as it does, between the Callunetum on the one hand and grassland merging into scrub on the other, contains transitional species from all three, and is never a pure community, but shares dominance with the dominant species of each of the others. On burnt areas, such as that to the north of summit plateau, its dominance is probably not continuous. This is, therefore, a temporary or transitional community.

The bilberry is seen at its best on the boundary banks traversing the mountain. Originally planted with a hawthorn hedge, these banks are now occupied by well-grown bilberry bushes, as the hawthorns, unable to retain sufficient hold on the dry and crumbling peat and exposed to devastating winds, have gradually succumbed, until only a comparatively few stunted bushes remain on the most sheltered bank in the slight dip between Wolfhill and Divis.

The flora is very similar to that of the transitional Callunetum, with a greater quantity of grasses and fewer bog plants.

VASCULAR PLANTS.

| | | | |
|-----------------------------|----|----------------------------|----|
| <i>Alchemilla vulgaris</i> | f. | <i>Fragaria vesca</i> | o. |
| (<i>Blechnum spicant</i>) | f. | <i>Galium saxatile</i> | a. |
| <i>Calluna vulgaris</i> | f. | <i>G. verum</i> | f. |
| <i>Carex caespitosus</i> | a. | <i>Hieracium pilosella</i> | f. |
| <i>Crataegus monogyna</i> | o. | <i>Hypericum pulchrum</i> | o. |
| <i>Deschampsia flexuosa</i> | a. | <i>Lathyrus montanus</i> | o. |
| <i>Digitalis purpurea</i> | o. | <i>Luzula campestris</i> | a. |
| <i>Erica cinerea</i> | o. | <i>L. sylvatica</i> | f. |
| <i>Festuca ovina</i> | a. | <i>Nardus stricta</i> | a. |

VASCULAR PLANTS (contd).

| | |
|----------------------------|------|
| <i>Poa annua</i> | a. |
| <i>Potentilla erecta</i> | f. |
| <i>Primula vulgaris</i> | o. |
| (<i>Pteris aquilina</i>) | r. |
| <i>Rosa canina</i> | o. |
| <i>Rubus fruticosus</i> | o. |
| <i>Rumex acetosella</i> | o. |
| <i>Salix aurita</i> | o. |
| <i>Scilla non-scripta</i> | o. |
| <i>Vaccinium myrtillus</i> | v.a. |
| <i>Viola canina</i> | o. |

MOSSES.

| | |
|---------------------------------|----|
| <i>Dicranum majus</i> | o. |
| <i>Hylocomium squarrosum</i> | a. |
| <i>Hypnum schreberi</i> | o. |
| <i>Polytrichum aloides</i> | o. |
| <i>Rhacomitrium fasciculare</i> | f. |
| <i>Thuidium tamariscinum</i> | o. |

LICHENS.

| | |
|---------------------------|----|
| <i>Cladonia coccifera</i> | o. |
| <i>C. pyxidata</i> | f. |

This community merges with hill pasture, but there is little change in flora save a greater abundance of grasses, and fewer ericaceous species.

SCRUB COMMUNITY.

Two facies of the scrub community are found. A dry heath scrub on the lower slopes east of Mount Gilbert, and a sheltered valley type dominated by *Corylus avellana* in Crow Glen. In the former, the shrubs are small and very stunted and they are either densely spinous near the ground or have their first branches about three feet up. *Crataegus* and *Prunus spinosa* are abundant, and willows are frequent. There are local patches of gorse (*Ulex*). The most definite patch of this scrub occurs to the left of the quarry, and here there is a dense undergrowth of *Calluna vulgaris*, *Vaccinium myrtillus* and many other heath types, in some cases growing as tall as the bushes. The smaller bushes have all a rounded appearance typical of close grazing, and some are overgrown with *Parmelia*. This scrub lies in the corner of a comparatively extensive pasture, the lower half of which is closely grazed by sheep. A second patch of scrub higher on the hill contains more tree-like forms of the same species, with occasional woodland types, such as *Rosa canina*, *Digitalis purpurea*, *Primula vulgaris* and *Scilla non-scripta*.

There seems to be little chance of the rejuvenation of this scrub when the present members die, as the close ground flora of ericaceous shrub leaves no room for the germination of seedlings and establishment of such in the surrounding grass areas is hindered by continuous grazing.

FLOWERING PLANTS.

| | | | |
|------------------------------|----|--------------------------------|----|
| <i>Ajuga reptans</i> | o. | (<i>Pteris aquilina</i>) | f. |
| <i>Anthoxanthum odoratum</i> | a. | <i>Prunus spinosa</i> | a. |
| (<i>Blechnum spicant</i>) | f. | <i>Pyrus aucuparia</i> (dwarf) | f. |
| <i>Calluna vulgaris</i> | f. | <i>Rosa canina</i> | r. |
| <i>Carex caespitosus</i> | a. | <i>Rubus fruticosus</i> | l. |
| <i>Crataegus monogyna</i> | a. | <i>R. idaeus</i> | r. |
| <i>Cytisus scoparius</i> | o. | <i>Salix aurita</i> | f. |
| <i>Erica cinerea</i> | f. | <i>Scilla non-scripta</i> | o. |
| <i>Festuca ovina</i> | f. | <i>Ulex europaeus</i> | l. |
| <i>Galium saxatile</i> | f. | <i>Vaccinium myrtillus</i> | f. |
| <i>G. verum</i> | f. | <i>Viola canina</i> | o. |
| <i>Hypericum pulchrum</i> | o. | | |
| <i>Lathyrus montanus</i> | f. | | |
| <i>Luzula campestris</i> | a. | | |
| <i>L. sylvatica</i> | f. | | |
| <i>Nardus stricta</i> | f. | | |
| <i>Poa annua</i> | f. | | |
| <i>Potentilla erecta</i> | f. | | |
| <i>Primula vulgaris</i> | o. | | |

MOSSES.

| | |
|-------------------------------|----|
| <i>Dicranella heteromalla</i> | o. |
| <i>Ditrichum homomallum</i> | o. |
| <i>Eurhynchium</i> spp. | o. |
| <i>Grimmia pulvinatum</i> | o. |
| <i>Hylocomium squarrosum</i> | a. |
| <i>Parmelia</i> spp. | f. |
| <i>Cladonia rangiferina</i> | o. |

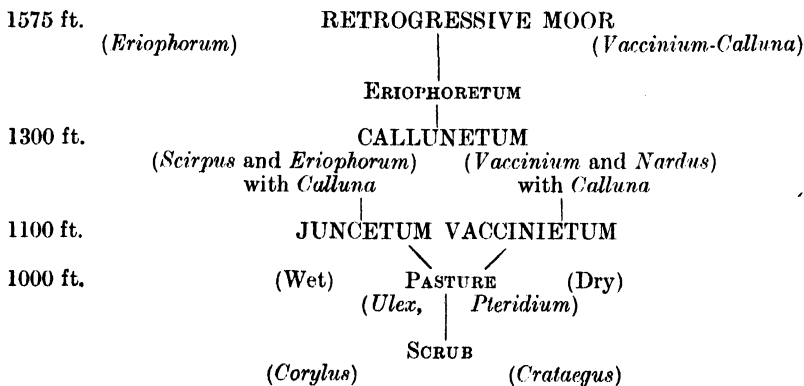
The *Corylus avellana* scrub dominates in Crow Glen, the valley of the Forth river, where the steep sides and the curve of the river give protection from the prevalent winds. Hazel and willow fringe the lower slopes and gradually merge with the hawthorn and gorse of the exposed valley top. This may be regarded as the remains of an Alder-Willow community. The undergrowth in the shade of the bushes is scanty and consists of ivy, liverworts and mosses, but the unshaded banks are fringed with woodland species included in the following typical list:

| FLOWERING PLANTS. | | | |
|--------------------------------------|------|--------------------------------|----|
| <i>Alnus glutinosus</i> | o.r. | <i>Prunus spinosa</i> | o. |
| <i>Carex</i> spp. | f. | <i>Ranunculus ficaria</i> | f. |
| <i>Chrysosplenium oppositifolium</i> | f. | <i>Rosa canina</i> | o. |
| <i>Corylus avellana</i> | a. | <i>Salix aurita</i> | a. |
| <i>Crataegus monogyna</i> | a. | <i>Ulex europæus</i> | a. |
| <i>Fraxinus excelsior</i> | o. | | |
| <i>Geranium robertianum</i> | o. | MOSSES. | |
| <i>Hedera helix</i> | f. | <i>Brachythecium rutabulum</i> | o. |
| <i>Lonicera periclymenum</i> | r. | <i>Campylopus flexuosus</i> | o. |
| <i>Luzula sylvatica</i> | a. | <i>Catharinea undulata</i> | o. |
| | | <i>Mnium hornum</i> | o. |

SUMMARY.

The various communities have been described in descending order of altitude; the following table shows the approximate zonation.

(N.B. The names of the chief communities are printed in capitals, the subordinate in smaller capitals, the societies and facies in brackets.)



In comparison with other mountain studies it is interesting to note that the chief communities are represented here either by associations or facies. That Eriophoretum and Vaccinietum are not well developed, is not remarkable, considering the extent of mountain under investigation. Pure Eriophoretum *vaginati*, as described by Moss (1913) (5) does not occur on Divis, nor does his "Sub-Alpine Grassland" unless the turf of the cairn mound may be considered a miniature equivalent. Otherwise, there is a distinct correlation between the zonation of Divis and Moss's "Table of Moorland Associations" for the Peak District.

EXAMINATION OF PEAT.

The plant remains in each sample were separated from the finer pollen material and placed in dishes labelled with their sample number. Samples 2-11 contained fragments of *Eriophorum*, samples 4 and 5 yielded remains of *Sphagnum*, *Hypnum* and *Racomitrium*, and samples 5-13 all contained parts of ericaceous plants, some of which were easily identified as *Calluna*.

In the examination of the pollen material 200 identified pollen grains were counted in each sample. The frequency of each species present is expressed as a percentage of the sum total of "forest-tree" pollen counted. *Corylus* and *Salix* are not counted as "forest-tree" pollens, and, according to the practice of continental workers, are expressed separately as percentages of the total of "forest-tree" pollens counted. *Corylus* is included in the pollen diagram. Ericaceous pollen was abundant in every sample, outnumbering every other species counted. The most abundant tree pollens found were those of birch, hazel and alder, and pine and oak pollens were also found in all samples. The occurrence of lime, elm and willow was sporadic.

In the samples from the lowest two levels, where the scarcity of pollen made it impossible to give comparative percentages, the only species identified was birch, which gradually increased in frequency in the younger layers and dominated the majority of the samples. Alder also has a higher frequency in the younger layers, while hazel, pine and oak have their maximum in the lower layers. The amount of pollen per sample increases up to sample 6 and then slightly decreases. Duplicate samples were submitted to Dr Erdtman, who reported on samples 4 and 6 with similar percentages to those recorded above.

There is great similarity with Erdtman's results for Scotland (11). The dominance of birch is well marked in both, and alder pollen reaches the same mean percentage frequency. The lower layers of Divis peat lie above Erdtman's "A" zone, the datum line for Scotland, taken at the level of the first appearance of alder, with a high percentage of pine and hazel pollen (circa 6000 B.C.). The decrease in frequency of pine and hazel pollen above this zone is general in Scotch peat, as is also the presence of oak, elm and lime in comparatively low percentages such as Divis peat exhibits.

The grouping of the pollen in the Pennine peat, as pictured in the pollen diagram for Warcock Hill (15), differs from Divis peat in two particulars: the absence of pine pollen in the upper layers and the high frequency of oak throughout. The only published peat diagram from Ireland is that of Claremorris peat (14), which is older than Divis peat. Above the "A" zone in the Claremorris diagram, the frequencies of the various species, though greater, are in approximately the same ratio, showing a decided dominance of birch in all layers.

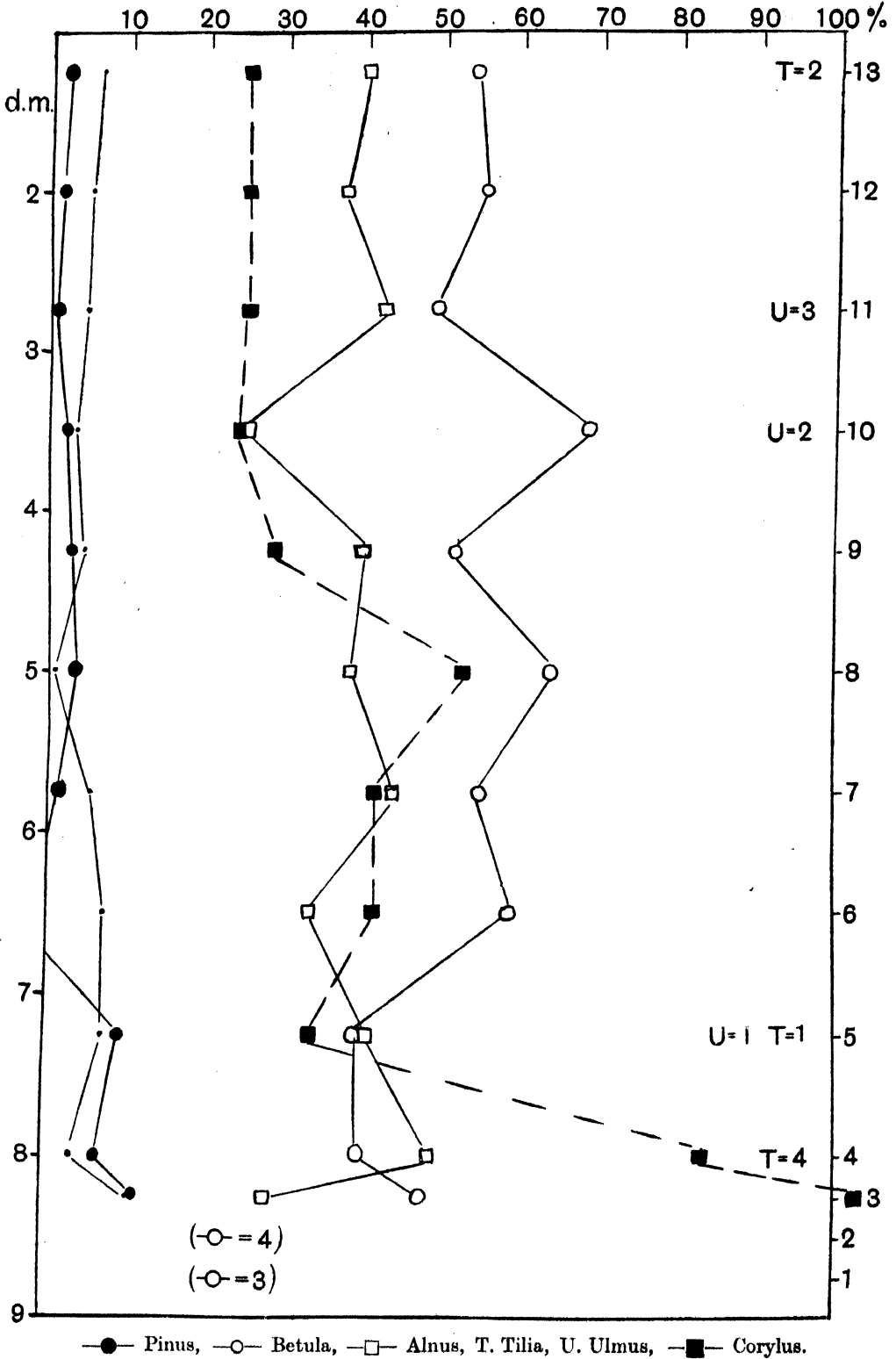


FIG. 3. Pollen diagram from Divis peat to a depth of 9 decimeters.

Erdtman (13) divides the formation of peat beds in Ireland into the following periods:

(1) The Earlier Marl Period. (Climate sub-arctic.) Tree growth scanty. Birch and willow dominant. Pine immigrant.

(2) The Later Marl Period. (Beginning of "Ancylus" period.) Immigration and rapid spread of hazel. Immigration of elm and oak.

(3) The Marsh-peat Period. (To the end of "Ancylus" period, 5400 B.C.) Peat of *Cladium*, etc. Maximum extent of pine forest. In the later part of this period alder immigrates and pine forests decrease.

(4) The Sphagnum-peat Period. ("Post-Ancylus" or "Atlantic" and "post-Atlantic" periods.)

(a) Period of increased alder forest.

(b) Period of secondary pine forest, max. in N. Ireland.

(c) Period of continuous decrease of pine.

(d) Period of deciduous trees, pine practically absent.

Erdtman also considers that the order of immigration of trees in Ireland is: birch, pine, hazel, elm, oak, alder, lime. All these tree pollens are present in Divis peat, with alder in high percentages in the lower layers, decreasing in frequency in the younger peat. This would indicate that the base of the Divis peat was formed during the Atlantic period (5200–2200 B.C.), probably at the beginning of Erdtman's "Sphagnum-peat period." Therefore the Divis peat would be equivalent in age to the Pennine and Swedish "post-Ancylus" peat deposits.

DISCUSSION.

As indications of the past flora of Divis we have the evidence of (1) buried wood and plant remains, (2) pollen statistics, (3) zonation, so far as it may be considered the epitome of succession, and (4) what might be termed "survivors" in the present flora.

The buried wood, found in the peat hags of the summit plateau, was identified as *Crataegus*. The form was greatly twisted and the outer wood somewhat disintegrated, the duramen deep red in colour. The wood was lying in the soft bared peat of the sides of the hags and there was no difficulty in its removal. A "hedge" of hawthorn grows on the north-south dyke, which is comparatively sheltered. These hawthorns were presumably planted and one would rather expect to find that a hedge had also been set in the east-west dyke, which crosses the summit plateau within a hundred yards of the wood remains. If so, the roots in this exposed position would be easily bared of the loose peat of the dyke and the bush overthrown and carried into the channels, where it would be buried by the fall of loose peat during erosion. No traces of the hypothetical hedge on this dyke have, however, as yet been discovered.

The view that the mountain top was originally covered with a community

similar to that described for the lower slopes of Mount Gilbert, has abundant confirmatory evidence. If *Crataegus* formed part of the original scrub association it would have been buried in the ordinary course of moor succession on poor soil and ultimately uncovered again by the weathering of the summit plateau. The evidence of the present flora and pollen analysis give weight to this theory. In the area of Callunetum near the summit there is an isolated patch of *Luzula sylvatica*, and near it a single dwarfed *Sorbus aucuparia*. On the northern slopes above the normal scrub limit there are numerous stunted hawthorns and another specimen of mountain ash. It is probable that these are survivors of a previously wide-spread scrub community rather than invaders of the "closed" community of *Calluna*.

In considering the pollen data, only the pollen present in high percentages may be fairly considered to give a clue to the past flora of the immediate neighbourhood. For though pollen statistics give a good idea of the past succession of woodlands over large areas, it is difficult to reconstruct the floral history of the smaller area of Divis, and to estimate what pollen has fallen from trees *in situ* and what has been contributed from neighbouring communities. However there is ample proof that certain trees were, for a period, able to live on, or near, the summit.

From the pollen investigations made there is evidence of a birch-alder-hazel scrub with ericaceous species in almost constant association. Pine and oak trees were present, probably in no great number or size, but well established within the limits of the Divis area. The sporadic occurrence of elm and lime pollen can scarcely be held to be evidence of their presence on the mountain itself.

The frequent remains of *Eriophorum* and the decrease in the general pollen frequency in the upper layers of the peat, indicate that this scrub period was followed by a wetter period which encouraged the formation of bog at the expense of the tree covering and so led to greater exposure of the area to the action of wind, rain and frost.

These agencies, together with drainage, have channelled out the peat and given the present peat-hag formation with *Eriophorum* and *Sphagnum* in the wet hollows, while *Calluna* and *Vaccinium* dominate the better drained hags.

As to zonation, the transition, from scrub on the lower slopes to the retrogressive moor of the summit, suggests this as the natural course of succession on the summit and the "neutral-grass" of the cairn as the ultimate extent of the succession at present. It is generally considered that existing grassland in Great Britain was originally forest clad, and, owing to the lowering of the tree limit and other causes, these woods have been superseded by a succession from scrub through moor to heath to grassland. This would be of little importance alone, but it is interesting in the light of the co-ordinating evidence from the investigation of pollen, wood remains and present flora.

That we might reconstruct the succession on Divis since the period pre-

ceding the beginning of the peat formation as starting with local birch and hazel scrub, the forest trees growing in more sheltered positions but at greater altitudes than their normal limit to-day. Then the heather gradually spread to the destruction of the woodland. This deforestation is hastened by the spread of *Eriophorum* and the moorland formation holds sway. Subsequently the surface of the peat is "weathered" into its present channelled state and the dominance of *Eriophorum* obscured by the development of *Vaccinium* and *Calluna* on the drier peat of the hags.

EVIDENCE OF FUTURE DEVELOPMENTS.

At present the degenerating peat area is extensive and will probably spread further into the Callunetum as the channels widen; and finally the remaining peat hags may be washed away, leaving bare area for re-invasion. If the denudation be complete, the "acidic-peat formation" may not appear again, but the moss-lichen association may invade the stone rubble as it has already invaded the bared area of the summit; while these peat plants still existing in the rock area will probably be gradually desiccated, unable to gain sufficient sustenance from the substratum.

At the same time, artificial drainage in the lower areas is checking the spread of *Eriophorum* and *Juncus* and turning these communities into pasture, where any possible successional changes will be barred by grazing. The effect of rabbits is never likely to be of serious account, as their numbers are kept down.

Callunetum is a relatively stable association, and as it is here encouraged for the benefit of the birds, there is no reason to expect any diminution in the future, except that its are will vary in inverse ratio to the spread of retrogressive moor. The abundance of *Calluna* seedlings on the upper slopes of Wolfhill indicate that the dominance is only temporarily obscured by burning.

The future history should be of particular interest, since this open moorland was strictly enclosed in the year 1925 in an attempt to rear grouse and make a game preserve of the Divis area.

In conclusion, acknowledgments are due to Professor J. Small, Department of Botany, Queen's University, Belfast, for suggesting the work and for his interest and assistance throughout its progress.

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THE EFFECTS OF EXPOSURE UPON THE STRUCTURE OF CERTAIN HEATH-PLANTS¹

BY D. N. E. BRIGHT, B.Sc., PH.D.

(With Plate XXXVI and ten Figures in the Text.)

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A. INTRODUCTION.

In the course of investigations on the heath association on Hindhead Common, a marked difference in the height of plants inhabiting the valleys and the tops of the ridges was noticed. This is very striking in the case of *Ulex nanus* (5, pp. 151-2), where tall plants are found only in the valleys and on the lower parts of the slopes, but it is also seen in most of the other members of the heath-flora. The frequent dying away of the tips of *Calluna* and *Ulex nanus* on the upper parts and tops of the slopes implied that the difference in stature might be due to the varying degree of exposure of the habitat. This view received further support from a comparison of other features, and Prof. Fritsch therefore suggested that I should endeavour to ascertain in how far increasing exposure was accompanied by morphological and anatomical differences.

¹ From the Botanical Department, East London College, University of London.

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For this purpose three plants with very diverse characteristics were selected, namely, *Pteridium aquilinum*, *Vaccinium Myrtillus*, and *Molinia coerulea*. Only the overground parts were taken into consideration and, in the case of *Vaccinium*, the young stem rather than the leaf was investigated, because it was thought likely to show more variation in response to diversity of habitat than the deciduous leaf. The investigation of the Bracken has been undertaken in greater detail than was possible in the case of the other two plants. The material was collected during the months of June to September, mostly in July, from 1922 to 1926.

Three typical specimens were selected at each point, and the overground portions were detached at ground-level. All material of the same species for any one year was gathered on the same day, and care was taken in selecting the specimens to ensure that they were all sun-forms. Most of the morphological comparison was carried out in the field during the months of June and July, when the exposure data mentioned below were obtained.

The percentage amounts of the different tissues, as seen in cross-section, were calculated from camera lucida drawings, the surface areas being determined by means of a planimeter.

B. THE NATURE OF THE "EXPOSURE" FACTORS.

Hindhead Common consists of a number of more or less flat-topped ridges, 750–850 feet above sea-level, intersected by several rather narrow valleys running in different directions, so that the slopes have diverse aspects. For the purpose of this investigation, material was gathered mainly from three slopes (see maps in 8, p. 35; 4, p. 346), viz.: the western slopes of the Central Ridge flanking the upper end of valley *A* with a W.N.W. aspect (squares 4 Z beyond the zone of *Ulex europaeus*, 3 A and 4 D), the Erica-slope at the southern end of the Central Ridge having a S.S.W. aspect (squares 20 A–21 A, 18 B, 15 D), and F 12 (4, p. 347), which has the same aspect and lies on the northern slope of valley *C*. Some material of *Vaccinium* was also taken from the slope facing the Erica-slope and having a N.N.E. aspect. The prevailing winds blow from the S.W., so that the valleys at the base of the Erica-slope and F 12 are very sheltered, whilst valley *A* is more exposed. Except on very windy days, however, little wind is to be noticed in any of the valleys which no doubt obtain further shelter from the large bushes, mainly of *Ulex europaeus*, that usually form a dense growth along the sides of the paths.

On the Erica-slope and F 12 the wind does not usually make itself felt until one has ascended about two-thirds of the slope, but F 12 and especially the valley at the base of it are much more sheltered than equivalent regions on the Erica-slope. On the western slopes of the Central Ridge near the top of valley *A* a breeze is felt at a rather low level, but at the top it is often not as strong as one would expect, perhaps because of the long flat stretch that lies in front of it in the southerly direction. The greatest degree of exposure

to wind is thus probably to be found at the top of the Erica-slope, next comes the top of F 12 and last the top of the northern end of the Central Ridge. As regards the valleys, valley *A* is probably most exposed, and that at the base of F 12 most sheltered, although there is probably not a great difference between it and the valley at the base of the Erica-slope.

For comparative purposes material of Bracken was also collected in July 1922 and 1924 from (*a*) near the point of junction of valleys *A* and *B*, where, owing to a very dense and extensive growth of large bushes, a very exceptional degree of shelter was obtained, (*b*) from the bare gravel stretches on the eastern slopes of the Central Ridge, where exposure to wind is not very marked but the substratum is very inhospitable, and (*c*) from a point near 12 on the base line, i.e. towards the top of the western slopes of the Central Ridge, where, prior to the fire of 1924, there was very luxuriant growth on a soil exceptionally rich in humus. Here considerable exposure was probably compensated by the rich water-content of the soil (8, p. 39).

The northern extremity of the Central Ridge in 1922, when the first specimens of the Bracken were collected, bore a rather dense growth of heath vegetation, some ten years old, that must have afforded appreciable shelter. In 1923, however, this region was completely burnt, so that the specimens gathered in 1924 had been growing under conditions of much greater exposure than those collected in 1922. The Erica-slope in 1922 bore a growth of heath about six years old and in proportion lower than that on the Central Ridge. On this slope there was a fire in 1924, so that the specimens gathered in that year came from ground which was almost completely bare of other growth. F 12 was similarly burnt in 1924; prior to the fire it bore dense vegetation about 12 years old. In 1925 and 1926 the heath association had begun to close up again on all these slopes. After burning the degree of exposure will be much greater, but at the different levels it is no doubt still in the same proportion (6, p. 124), as shown by evaporation data.

A few attempts were made to compare the strength of the wind at the bases and tops of the slopes in 1925. Two identical anemometers which had previously been calibrated were used simultaneously, being placed in a straight line with one another, one at the base, the other at the top of the slope, the fans facing the direction of the wind.

Each anemometer was watched closely over a period of 40 minutes, during which time any deflection of the needle was recorded. On examining the records obtained at the base and top of the Central Ridge, it was found that during the period there were 46 deflections at the base of the slope while at the top there were 178, further at the base the total sum of the deflections was 417° while at the top of the slope it was 1029° .

Two days later this was repeated on F 12, but on a calmer day, so that no comparison can be made between the two slopes. At the base there were 11 deflections during a period of 40 minutes and at the top 168, while the total

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sum of the deflections was 20.5° , and 672° respectively. These figures show the great difference between the wind-intensity at the base and top of the slopes.

A rather more indirect estimate of the wind-effect can be obtained by determining the rate of evaporation at different levels on the slopes, but there was no opportunity of collecting more than a few data of this kind. In June and July 1925 when, owing to recent fires, the areas under investigation bore very little growth, atmometer cups attached to burettes were placed so that the middle of the cup was at the average heights above ground-level of the bracken fronds at each spot. Readings were taken after three hours' exposure, usually at 1 p.m. and 4 p.m. (Table I). They show that the evaporating power of the air is frequently greater at the top than at the base of the slope, although,

Table I. *Evaporation (in c.c.) at different levels on the slopes, June, 1925.*

| Position | Time | Atmometer readings | | | |
|---------------|--------|--------------------|-------------|-------------|-------------|
| | | 1. vi. 1925 | 2. vi. 1925 | 3. vi. 1925 | 4. vi. 1925 |
| Central Ridge | Base | 10-1 | — | 3.5 | — |
| | | 1-4 | — | 11.2 | — |
| | Middle | 10-1 | — | 5.3 | — |
| | | 1-4 | — | 8.6 | — |
| | Top | 10-1 | — | 5.2 | — |
| | | 1-4 | — | 8.6 | — |
| Erica-slope | Base | 10-1 | — | — | 7.1 |
| | | 1-4 | 5.9 | — | 9.3 |
| | Middle | 10-1 | — | — | 9.1 |
| | | 1-4 | 7.32 | — | 8.9 |
| | Top | 10-1 | — | — | 9.6 |
| | | 1-4 | 7.9 | — | 10.4 |
| F 12 | Base | 10-1 | — | 5.4 | 8.9 |
| | | 1-4 | — | 8.6 | 9.7 |
| | Top | 10-1 | — | 5.7 | 9.8 |
| | | 1-4 | — | 9.8 | 10.7 |
| | | 10-1 | — | — | — |
| | | 1-4 | — | — | — |

especially in the case of F 12, the differences are not very marked. On the Central Ridge moreover the evaporating power of the air on the days of these investigations was often less at the top than at the base. These results accord with those obtained by Fritsch and Salisbury (6, p. 124) for F 12 and the Central Ridge (F 11), and indicate clearly that the conditions of exposure on the latter, with its westerly aspect, are not altogether the same as those on the slopes facing south. It should be noted, however, that their and my data refer to recently burnt areas. Dr F. M. Haines, who has made numerous estimates of evaporation at 9-12 in. above the soil on the slope of the Central Ridge extending down to valley A and on the Erica-slope, informs me that in practically all cases they show a marked increase in evaporating power at the top as compared with the base. His results, however, are averages for several days and thus do not show the minor fluctuations above referred to.

In June of 1925 a few wet and dry bulb readings were taken at hourly intervals (between eleven and four), the thermometers being fixed at the average level of the *Pteridium* fronds on the different parts of the slopes.

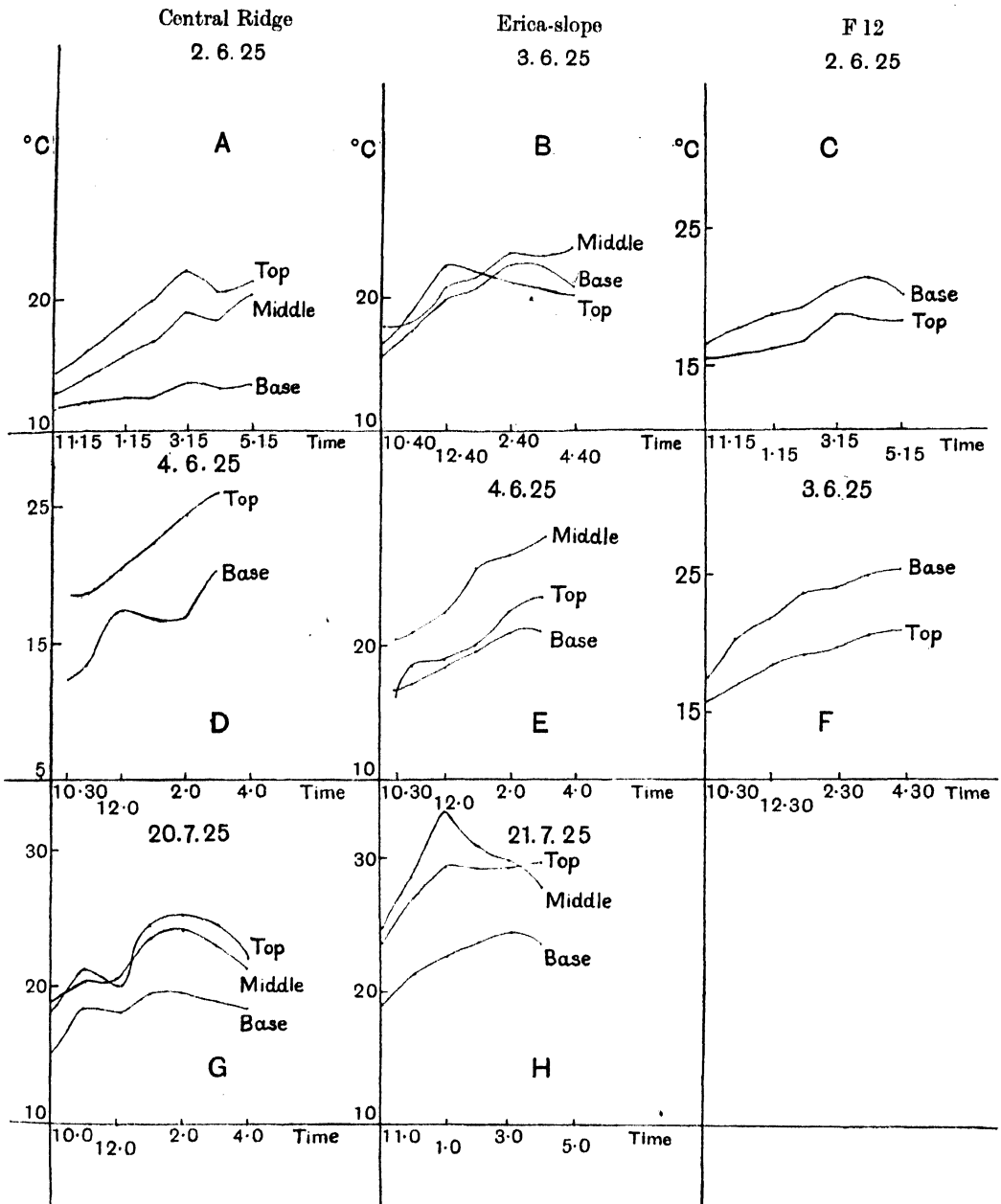


FIG. 1. Graphs showing the variations in soil temperature at a depth of 5 cm. at the base, middle, and top of three slopes. Graphs for the same slope are placed vertically above one another.

The results indicate that the percentage humidity of the air at such times is greater at the top than at the base of F 12 and the Central Ridge, but on the Erica-slope this is only the case until midday, after which the greater

percentage is found at the base until after 3 p.m. I am indebted to Dr Haines for further data confirming the results as regards percentage humidity of the air on the Erica-slope. His readings were taken in July at 6 in. and 3 ft. levels and afforded the same contrast between the morning and afternoon. It must be borne in mind that these data refer only to the midsummer period and at other times of the year might be different.

Varying exposure may also be expected to affect the temperature of the soil, and data¹ on this point were collected on the same days and from the same spots as the atmometer readings above considered. On each slope three thermometers were used simultaneously, the bulbs being buried to a depth of 5 cm. below the surface, while the stems were covered with a wooden casing; readings were taken every hour. The rather variable results are shown graphically (Fig. 1). In the case of F 12 both graphs run practically parallel, the base always affording the higher readings, but this was not borne out on the Central Ridge or the Erica-slope. On these the base of the slope usually showed lower temperatures than either the middle or the top. Attention may be drawn to the fact that the middle of the Erica-slope often affords the highest soil temperatures.

The data above given support the view of more stringent conditions in relation to transpiration at the tops than at the bases of the slopes, although the middles of the slopes do not always fall into line and there are other aberrant results which probably depend on the varied exposure of the different slopes.

It is, however, impossible to separate such exposure effects from the effects of soil differences, such as occur at the different levels on the slopes. The valleys always have a higher water- and humus-content (8, pp. 47, 57) and mostly a higher salt-content, though the middles of the slopes are commonly aberrant (8, p. 57). This matter is considered more fully in the concluding section, but it may be pointed out that the morphological and anatomical differences detailed below are probably in part a result of these soil differences, which may indeed perhaps in some cases be of greater importance than the differences of exposure.

C. THE LEAF OF *PTERIDIUM AQUILINUM*.

(a) MORPHOLOGY.

The leaf of *Pteridium aquilinum* consists of a usually erect petiole and the lamina, which forms a variable angle with the vertical. The leaf, on the area of ground under consideration, may vary from 15 to 150 cm. in height, the petiole occupying roughly half of this. In the lamina the pinnae are produced

¹ Since the areas were quite recently burnt, the results refer to young heath.

in successive pairs, which are not however always exactly opposite one another. Each pinna resembles a minute frond, although the basal stalk is relatively much shorter; the pinnae may be bi- or tripinnate. The pinnae and their subdivisions do not spread out in one plane, their position in relation to the main petiole varying with the degree of exposure of the frond (see p. 337).

The petiole is roughly cylindrical, but its overground portion flattens out on the adaxial side, the plane of the flattening being at right angles to the direction of inclination of the lamina. Two small greenish-white ridges, the "lateral lines," extend up the flanks of the petiole, close to and one on either side of the flattened upper surface (see Fig. 5 *E, l*), their position being practically constant. Where the first pinnae arise, the lateral line bends outwards along the stalk of the pinna until a pinnule is reached. Here the lateral line again alters its course so as to pass along the stalk of the pinnule, at the base of whose lamina it appears to end blindly. The lateral lines are always two in number and in all parts of the frond occupy the same position facing upwards as in the main petiole.

Observations made at Hindhead from time to time have shown that specimens sheltered from the wind possess a more extensive and spreading lamina than those from very exposed positions which appear dwarfed. In these respects the two kinds of specimens resemble shade- and sun-forms (3, p. 228) respectively, but all my plants were sun-forms. Boodle (1, p. 660) remarks of *Pteridium aquilinum* "that in exposed plants... the subdivision of the secondary pinnae is usually not carried so far" as in the sheltered forms. In the specimens I examined it was obvious that the subdivision of the pinnules, in the wind-sheltered specimens, is carried further than in those that are subjected to great exposure.

The external features of the frond most liable to vary are: (i) height above ground; (ii) height of petiole; (iii) surface area of lamina; (iv) angle made by lamina with petiole; (v) position of frond in relation to wind; (vi) position of pinnules; (vii) insertion of pinnae and pinnules; (viii) subdivision of pinnules; (ix) time of ripening of sori.

(b) ANATOMY.

1. *Petiole*. In transverse section the petiole is bounded by a thick-walled epidermis composed of small cells with scanty, colourless living contents and rounded or oblong cell cavities (Fig. 2 *C, ep.*). The cells are elongated, being about six times as long as wide. The outer walls are convex, strongly thickened and stratified, while all the walls are deeply pigmented, their colour varying from a light yellow to a dark blackish brown. The extent to which the walls are thickened and impregnated with this coloured substance varies considerably even in adjacent cells, but, so far as can be seen, this variation is indiscriminate. The cuticle is especially plain in the cells which are not so strongly thickened or so deeply coloured.

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Situated immediately within the epidermis are several layers of polygonal fibres with scanty granular contents and separated by extremely small inter-cellular spaces (Fig. 2 *C*, *sc.*). The outer layers are made up of small cells with thick brown walls, coloured brown by phlobaphenes in a similar way to the

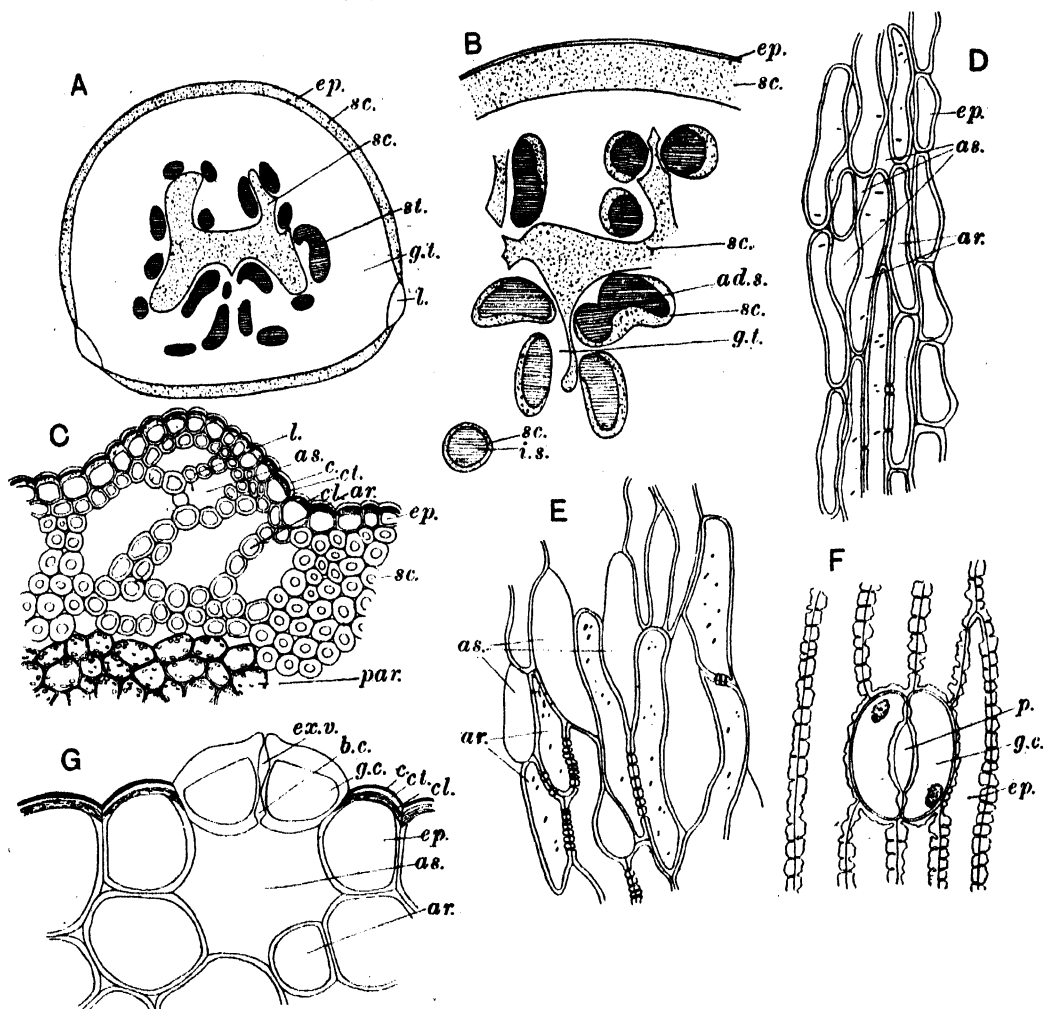


FIG. 2. *Pteridium aquilinum*, petiole. A, transverse section; B, portion of A enlarged; C, transverse section through the lateral line; D, radial longitudinal, and E, tangential longitudinal sections of the same; F, stoma of lateral line in surface view; G, the same in transverse section. *ad.s.*, *i.s.*, and *st.* meristele; *ar.* aerenchyma; *as.* air-spaces; *b.c.* back cavity; *c.* cuticle; *cl.* cellulose layer of epidermis; *cl.* cuticularised layer of same; *ep.* epidermis; *ex.v.* external vestibule; *g.c.* guard-cell; *g.t.* ground tissue; *l.* lateral line; *par.* storage parenchyma; *sc.* sclerenchyma.

epidermal cells. Toward the interior the average cross-section of the fibres increases, while the walls usually decrease in thickness and are not so deeply coloured. There is often a more or less perfect gradation in size and colouring from the dark small-celled outer layers of the stereom band to the large

colourless cells which border on the ground tissue. In longitudinal sections the fibres are on an average 30 times as long as broad; they have blunt ends, and all their walls bear numerous simple, slit-shaped pits placed either transversely or obliquely. The contents include numbers of nuclei of irregular shape.

The stereom band is interrupted at two points by the above-mentioned "lateral lines" (Fig. 2 *A*, *l.*). In transverse section the latter are formed by wedge-shaped masses of thick-walled cells extending from the epidermis to the inner cortex and of about the same depth as the stereom band (Fig. 2 *C*). They stand out clearly from the surrounding sclerenchyma, since their walls are not quite so strongly thickened or so deeply coloured. The constituent cells are more or less circular in cross-section and have dense protoplasmic contents without chloroplasts. They are separated by abundant large air-spaces (see Fig. 2 *C*, *as.*) communicating with the external atmosphere by means of normal stomata in the overlying epidermis which at these points shows the same characteristics as elsewhere. The intercellular spaces of the lateral line form a network similar to that found in the mesophyll of the pinnule; they are much broader in the tangential than in the radial direction (cf. Fig. 2 *D* and *E*). In radial longitudinal section the lateral line consists of about six rows of short thick-walled cells with broad ends and roughly two-and-a-half times as long as they are wide; they bear numerous simple pits upon all their walls (Fig. 2 *D*). In tangential longitudinal section the cells form a framework, a mesh of which underlies each stoma (Fig. 2 *E*).

The stomata are placed with their pores parallel to the long axis of the petiole. They are roughly equal in breadth to, and resemble in general structure, the stomata of the pinnules, but they are half as long again. They are slightly raised above the level of the adjacent epidermis (Fig. 2 *G*). In surface sections of the lateral line they are seen to be scattered in an irregular fashion at rather wide intervals. The lateral line thus constitutes an interruption in the stereom band whereby direct contact between the central region of the petiole and the outside atmosphere is established.

The remainder of the ground tissue is composed of large thin-walled cells rich in starch and having lignified walls bearing simple slit-shaped pits; there are numerous small intercellular spaces. The numerous more or less elliptical meristeles (18, p. 10) are arranged approximately in the form of an Ω with the opening towards the adaxial surface, except that the convex margin is invaginated (Fig. 2 *A*). This arrangement remains constant throughout the petiole up to the point of origin of the first pinnae. The meristeles form a network, as described by Tansley and Lulham (18, p. 14).

Within the zone of steles and occupying the very centre of the petiole is an irregular mass of sclerenchyma of varied extent. Meristeles, not in close contact with the central stereom, are completely encircled by one or more layers of similar thick-walled cells lying immediately external to the

endodermis. In steles directly adjacent to the stereom, however, thick-walled elements are usually found only on the distal side (Fig. 2 B). The central sclerenchyma may be either continuous or broken up into strands, each separated from the other by a narrow stretch of thin-walled ground tissue. The cells are like those of the peripheral stereom and are separated by very small intercellular spaces, the thick walls being bright yellow to deep brown, although this colour disappears towards the top of the petiole. The central sclerenchyma constitutes an axial rod extending throughout the length of the petiole, and its degree of development varies with the exposure, the amount tending to decrease with an increase of shelter.

As regards the individual steles, the endodermis is composed of small tabular cells with prominent nuclei and brown contents and with the inner tangential walls slightly thickened. The pericycle is a single layer of rather larger thin-walled elements with colourless living contents. These layers surround the usual zones of phloem and xylem, the structure of which is too well known to require description.

The anatomical features of the petiole most liable to vary are: (i) area of cross-section; (ii) percentage of sclerenchyma; (iii) percentage of steles; (iv) thickness of outer epidermal walls; (v) thickness of walls of sclerenchyma; (vi) width of lumen of xylem elements.

2. *Pinnule*. A transverse section, cut half-way between the stalk and the tip of a pinnule gathered in July, shows the lamina to be convex-concave, with the margins harbouring the sori strongly inrolled towards the under surface. The position of the mid-rib is indicated on the under surface by a very well-defined ridge extending throughout the length of the pinnule (cf. Fig. 4).

The upper epidermis is devoid of hairs and stomata and all its walls are more or less uniformly thickened; there is a well-defined cuticle. In transverse section (cf. Fig. 3 A, *u.ep.*) the cells vary greatly in size and shape, some being small and isodiametric, while others are broadened in the transverse direction. They have prominent nuclei, and no chloroplasts, though, according to Woodhead (20, p. 371), chloroplasts occur in the epidermal cells of leaves growing in deep shade. In surface view they are more or less isodiametric, with thick undulating lateral walls composed of cellulose (Fig. 3 B).

Beneath the upper epidermis is a hypoderm with scanty living contents which is often not continuous (Fig. 3 A, *hy.*), and extends from the mid-rib to the neighbourhood of the sori, where it dies out. Its degree of development is not determined by varied exposure. In transverse section its cells are circular or tabular and, in the latter case, often produced on their inner sides into a number of lobes which penetrate between the adjacent palisade cells (Fig. 3 A, *hy.*); in surface sections they are elongated parallel to the mid-rib. All the walls are thick and of cellulose and studded with numerous simple pits (Fig. 3 C). There is no hypoderm beneath the lower epidermis.

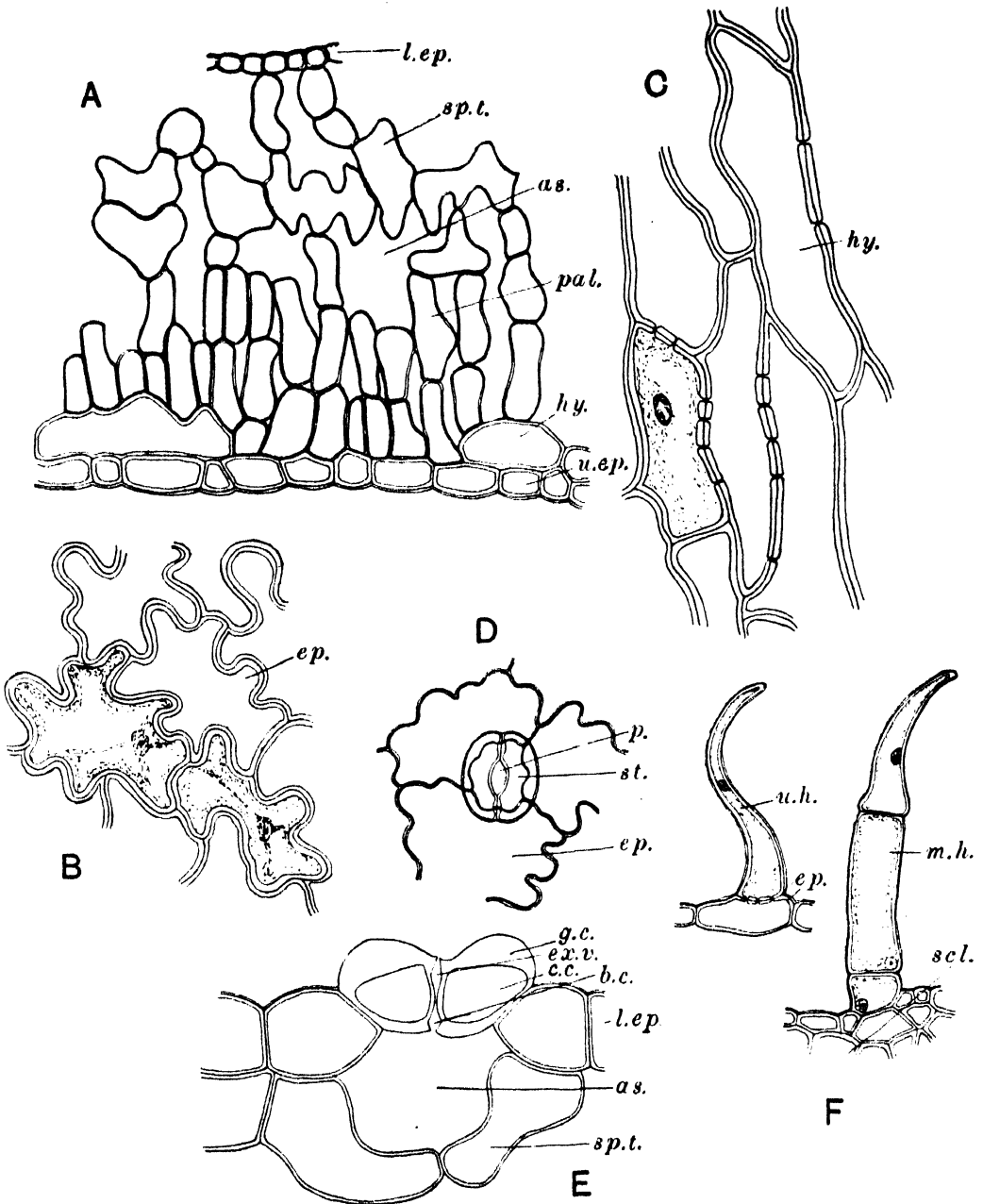


FIG. 3. *Pteridium aquilinum*, pinnule. A, transverse section through a portion between two veins; B, upper epidermal cells in surface view; C, surface view of hypoderm; D, stoma in surface view with the underlying epidermal cells; E, transverse section of stoma; F, hairs found on the lower epidermis. as. air-spaces; b.c. back cavity; c.c. cell cavity; ep. epidermal cell; ex.v. external vestibule; g.c. guard-cell; hy. hypoderm; l.ep. lower epidermis; m.h. multicellular hair; p. pore; pal. palisade; scl. sclerenchyma; sp.t. lobed cells of spongy tissue; st. stoma; u.ep. upper epidermis; u.h. unicellular hair.

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The vascular system of the mid-rib is embedded in a wedge-shaped mass of thick-walled fibres which extends from the upper to the lower epidermis (Fig. 4, *r.*), but along the flanks thins out to a single layer. The component cells are polygonal with small intercellular spaces, and resemble the sclerenchyma of the petiole, but the walls are white and shining and devoid of any colouring matter. Three layers are distinguishable, by appropriate tests, in these walls, viz.: middle lamella, lignified layer, and an innermost cellulose layer. On the upper side of the pinnule, adjacent to the furrow, the cells are

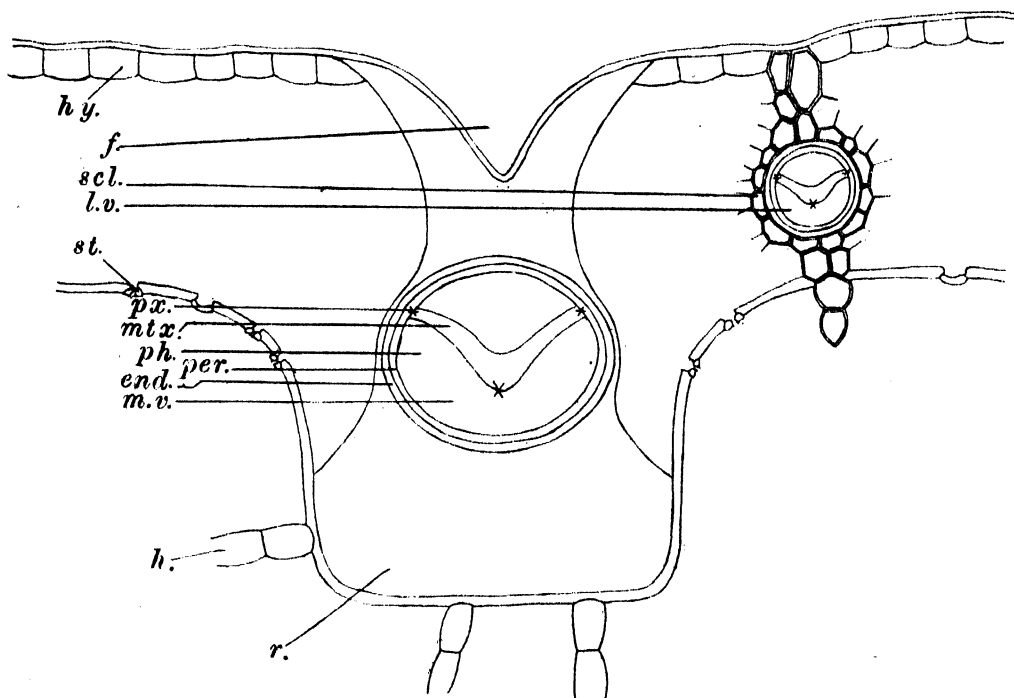


FIG. 4. *Pteridium aquilinum*, transverse section of pinnule in the region of the median vein. *end.* endodermis; *f.* furrow; *h.* hairs; *hy.* hypodermis; *l.v.* lateral vein; *mtx.* metaxylem; *m.v.* median vein; *per.* pericycle; *ph.* phloem; *px.* protoxylem; *r.* ridge; *scl.* sclerenchyma; *st.* stoma.

smaller, the lignified layer is much thicker than the cellulose layer, and the cell cavities are very small. On the other hand, on the lower surface, in the region of the ridge, the cellulose layer seems to predominate and the cell cavities are large and occupied by numerous starch grains. The irregular shape of the nuclei and the granular protoplasm probably indicate that these cells are moribund. The contents present the same appearance in freshly gathered material. A similar, but less extensive, investment of strengthening tissue is developed around the smaller veins (Fig. 4) which vary in number according to the degree of forking of the laterals of the first order.

The vascular system of the mid-rib is composed of a central V-shaped mass of tracheids, the point of the V facing downwards and the arms extending as

far as the one-layered pericycle. There are three groups of protoxylem (Fig. 4, *px.*), one at the end of each arm and the third at the point of the V. Phloem, composed of sieve-tubes and parenchyma, lies both above and below the xylem. The endodermis is similar in character to that of the petiole (cf. p. 332).

The mesophyll is extremely variable, but the variations do not appear to be related to the changes in habitats here studied. The palisade tissue is composed of one, two (Fig. 3 *A*), or more layers of columnar cells, but in the neighbourhood of the sori these cells gradually decrease in length until they are indistinguishable from the spongy tissue. At its lower limit the palisade tissue in some cases grades over into a region of broad extensively lobed cells (Fig. 3 *A*), the intercellular spaces of which enlarge as one approaches the lower epidermis, where these cells give place to a spongy tissue whose cells are rounded as seen in transverse section. In other cases the palisade is followed immediately by the latter type of tissue, the lobed cells being entirely absent. The latter exhibit production into lobes both in transverse and surface sections, while the rounded spongy cells are only lobed in the plane parallel to the epidermis.

The cells of the lower epidermis are essentially like those of the upper, though smaller and provided with a thinner cuticle. In the neighbourhood of the veins the lower surface of the pinnule bears thick-walled, pointed, unicellular and multicellular hairs provided with a well-defined cuticle; the constituent cells have large nuclei and scanty protoplasmic contents (Fig. 3 *F*).

The stomata are markedly raised above the general level of the lower epidermis; this is a constant feature in all the specimens examined. In transverse section (Fig. 3 *E*) the guard-cells appear small and somewhat elliptical, with strongly thickened walls and a slightly oblique lumen; the outer walls are more strongly thickened than the others. At the outer and inner edge of the pore the thick wall is produced into two beak-like processes. In surface view (Fig. 3 *D*) the stomata overlie the adjacent epidermal cells and are arranged with their long axes parallel to that of the pinnule, i.e. parallel with the median vein. The pore is oval in surface view.

The features of the pinnule most liable to vary are: (i) thickness of pinnule; (ii) characters of mesophyll; (iii) width and length of palisade cells; (iv) volume of palisade cells; (v) hypoderm; (vi) number of stomata per unit area.

(c) COMPARATIVE CONSIDERATION OF THE MORPHOLOGICAL FEATURES OF THE FRONDS IN SPECIMENS FROM HABITATS OF VARYING EXPOSURE.

The height of the frond varied from 15 cm. in an exposed region (*viz.* the top of the Central Ridge) to 150 cm. in the most sheltered spot on the area (the junction of valleys *A* and *B*); while the petiole (measured from ground-

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level to the point of origin of the first pinnae) varied from 5 cm. at the top of the Central Ridge to 74 cm. at the junction of valleys *A* and *B*. The height of the entire frond, as well as of the petiole, invariably shows a gradual decrease as one ascends the slopes. In 1924, however, on the *Erica*-slope, the smallest fronds occurred half-way up, although this irregularity was not

Table II. *Comparison of the morphological features of fronds of Pteridium aquilinum.*

(All observations made in July of the respective years; averages of 50 specimens in each case.)

| Position | Year | Height of fronds (cm.) | Height of petiole (cm.) | Diameter of petiole (cm.) | Angle of lamina with petiole in degrees* | No. of pinnae per frond | |
|---------------------------|--|------------------------------|-------------------------------|---------------------------------|---|-------------------------------|-----------------|
| <i>Erica</i> -slope | Base | 1924 | 46.4 | 23.7 | 0.65 | 33 ² | 21 |
| | | 1925 | 58.9 | 28.9 | 0.60 | 12.3 ¹ | 23 |
| | | 1926 | 54.5 | 34.8 | — | — | — |
| | Middle | 1924 | 30.4 | 15.4 | 0.44 | 18 ¹ | 16 |
| | | 1925 | 36.1 | 15.4 | 0.46 | 20 ¹ | 21 |
| | | 1926 | 40.9 | 21.2 | — | — | — |
| | Top | 1924 | 42.6 | 22.7 | 0.41 | 12 ¹ | 13 |
| | | 1925 | 32.0 | 12.0 | 0.39 | 13.9 ¹ | 22 |
| | | 1926 | 34.7 | 14.8 | — | — | — |
| Central Ridge | Base | 1924 | 56.3 | 31.2 | 0.57 | 14 ¹ | 19 |
| | | 1925 | 52.8 | 21.3 | 0.59 | 12.6 ¹ | 27 |
| | | 1926 | 51.5 | 22.1 | — | — | — |
| | Middle | 1924 | 36.6 | 15.3 | 0.48 | 26 ¹ | 15 |
| | | 1925 | 47.8 | 18.9 | 0.52 | 13.1 ¹ | 26 |
| | | 1926 | 40.0 | 21.7 | — | — | — |
| | Top | 1924 | 33.7 | 14.8 | 0.36 | 30 ¹ | 13 |
| | | 1925 | 33.0 | 14.5 | 0.38 | 11.7 ¹ | 17 |
| | | 1926 | 36.2 | 18.2 | — | — | — |
| F 12 | Base | 1924 | 44.5 | 21.9 | 0.56 | 32 ¹ | 18 |
| | | 1925 | 57.2 | 24.1 | 0.67 | 16.7 ² | 24 |
| | Top | 1924 | 37.3 | 16.5 | 0.51 | 18 ¹ | 14 |
| | | 1925 | 41.9 | 15.8 | 0.49 | 17 ¹ | 21 |
| | Junction of valleys <i>A</i> and <i>B</i> | | 1924 | 113.1 | 46.5 | 0.88 | 37 ² |
| From near 12 | | 1924 | 46.2 | 24.2 | 0.68 | 23 ² | 20 |
| Gravel in valley <i>B</i> | | 1924 | 38.9 | 20.1 | 0.56 | 16 ¹ | 18 |

* I.e. angle between petiole and plane of first set of pinnae at which bending of the frond was apparent. The indices denote where bending occurred, i.e.

16¹ = \angle of 16° made by lamina with petiole at point of origin of first pair of pinnae,

16² = \angle of 16° made by lamina with petiole at point of origin of third pair of pinnae.

observed in 1925 or 1926. The diameter of the petiole, as measured at ground-level, likewise shows a reduction with increased exposure. The data illustrating these points are given in Table II. Attention may be drawn to the frequent marked correspondence of the figures for the same habitat in successive years, and to the fact that the height of the petiole does not vary in direct proportion to that of the entire frond.



Pteridium aquilinum. Fronds in side view silhouette (on the left) and in front view (on the right); above from the base and below from the top of the Central Ridge.

The distance between the first and second, second and third, third and fourth sets of pinnae decreases progressively as one passes up the slopes (Table III). In Table IV, where the distance between the first and second, second and third, third and fourth pairs of pinnae at the bases of slopes are taken as 1, those at the middle and top of the Central Ridge are always approximately 0.65 and 0.59 of those at the base; those on the Erica-slope are 0.7 and 0.58 respectively. On F 12 those at the top of the slope are approximately 0.61 of those at the base. In Table V, where the distance between the first and second pairs of pinnae is always taken as 1, the relative distance between the second and third, and third and fourth pairs is seen to be approximately a constant, 0.75 and 0.54 respectively. These data serve to show that the different parts of the rachis vary proportionally to one another according to their position on the slopes.

The number of pinnae per frond decreases as one progresses up the slope (Table II). The fronds in the exposed positions are therefore of smaller stature and produce fewer pinnae than their fellows in the sheltered valleys.

The lengths of the lowest pair of pinnae (Table III) decrease with increased exposure, except on the Erica-slope where the shortest pinnae were found in the middle of the slope. These results were obtained in 1925 and are remarkable because these specimens are not the lowest in stature (Table II), as they were in 1924.

A cursory glance at the fronds in 1924, just after the ground had been laid bare by extensive fires, conveyed the impression that the angle between an imaginary continuation of the petiole, which is practically always vertical, and the plane of the lamina varied according to the position of the frond upon the slope. When an attempt was made to measure this angle one was confronted with the difficulty that successive pairs of pinnae usually make an increasing angle with the vertical; moreover, whilst in many cases the plane of the first pair of pinnae was already inclined, in other fronds such an inclination was only obvious at the point of origin of the second or third pairs. The point at which bending first occurred was determined by inspection of the frond, and at this point the angle with the vertical was measured. The relevant data, which are given in Table II, only express therefore the angle of inclination at the first point of bending of the frond and not of the whole frond.

In specimens near the tops bending was generally slight (cf. however, the Central Ridge in 1924, where the opposite obtains) and occurred mainly at the points of origin of the three lowest pairs of pinnae (Fig. 5 *D*), whilst in specimens from the bases of the slopes bending was pronounced and increased in amount at the point of origin of each pair of pinnae (Fig. 5 *B*). There was thus a very apparent difference between the side view silhouettes of the fronds at the top and base of the slope (cf. Pl. XXXVI).

In 1924 exposed fronds were always placed so that the laminae bent towards the direction of the prevailing winds, whereas in sheltered specimens

Table III. *Measurements of lamina of Pteridium aquilinum (July 1925).*

(Average of 50 specimens in each case.)

| Position | Distance between 1st and 2nd sets of pinnae (cm.) | Distance between 2nd and 3rd sets of pinnae (cm.) | Distance between 3rd and 4th sets of pinnae (cm.) | Length of lowest left pinna (cm.) | Length of lowest right pinna (cm.) |
|---------------|---|---|---|--|---|
| Erica-slope | | | | | |
| Base | 11.3 | 8.6 | 6.4 | 23.4 | 24.4 |
| Middle | 7.5 | 5.6 | 4.1 | 17.9 | 18.3 |
| Top | 6.6 | 5.1 | 3.6 | 20.8 | 20.5 |
| Central Ridge | | | | | |
| Base | 12.2 | 9.4 | 7.4 | 26.3 | 26.7 |
| Middle | 9.4 | 6.9 | 4.8 | 23.2 | 25.1 |
| Top | 7.6 | 5.6 | 3.8 | 16.5 | 17.8 |
| F 12 | | | | | |
| Base | 11.4 | 8.1 | 5.8 | 26.8 | 28.3 |
| Top | 6.9 | 5.1 | 3.8 | 18.5 | 18.8 |

Table IV. *Measurements of lamina of Pteridium aquilinum (July 1925).*

Ratios of distances between the 1st, 2nd and 3rd pairs of pinnae, assuming that the space between 1st and 2nd, 2nd and 3rd, 3rd and 4th at bases of slopes is 1. Distance measured from first point of branching towards tip of frond. Average of 50 specimens in each case.

| Position | Distance between 1st and 2nd sets of pinnae | Distance between 2nd and 3rd sets of pinnae | Distance between 3rd and 4th sets of pinnae |
|---------------|--|--|--|
| Erica-slope | | | |
| Base | 1 | 1 | 1 |
| Middle | 0.66 | 0.66 | 0.64 |
| Top | 0.58 | 0.60 | 0.58 |
| Central Ridge | | | |
| Base | 1 | 1 | 1 |
| Middle | 0.71 | 0.73 | 0.66 |
| Top | 0.62 | 0.58 | 0.53 |
| F 12 | | | |
| Base | 1 | 1 | 1 |
| Top | 0.59 | 0.61 | 0.64 |

Table V. *Measurements of lamina of Pteridium aquilinum (July 1925).*

Ratios of distances between 1st, 2nd and 3rd pairs of pinnae, assuming that the distances between the 1st and 2nd sets of pinnae are always 1. Average of 50 specimens in each case.

| Position | Distance between 1st and 2nd sets of pinnae | Distance between 2nd and 3rd sets of pinnae | Distance between 3rd and 4th sets of pinnae |
|---------------|--|--|--|
| Erica-slope | | | |
| Base | 1 | 0.75 | 0.56 |
| Middle | 1 | 0.75 | 0.54 |
| Top | 1 | 0.78 | 0.56 |
| Central Ridge | | | |
| Base | 1 | 0.77 | 0.60 |
| Middle | 1 | 0.73 | 0.51 |
| Top | 1 | 0.73 | 0.51 |
| F 12 | | | |
| Base | 1 | 0.71 | 0.51 |
| Top | 1 | 0.74 | 0.55 |

the direction of bending was haphazard. In 1925 this was less marked and in 1926 there was no uniformity about the orientation of the fronds at any level on the slopes. It must be noted that the surrounding heath vegetation in 1925 was growing apace and in 1926 formed an effective buffer to the wind

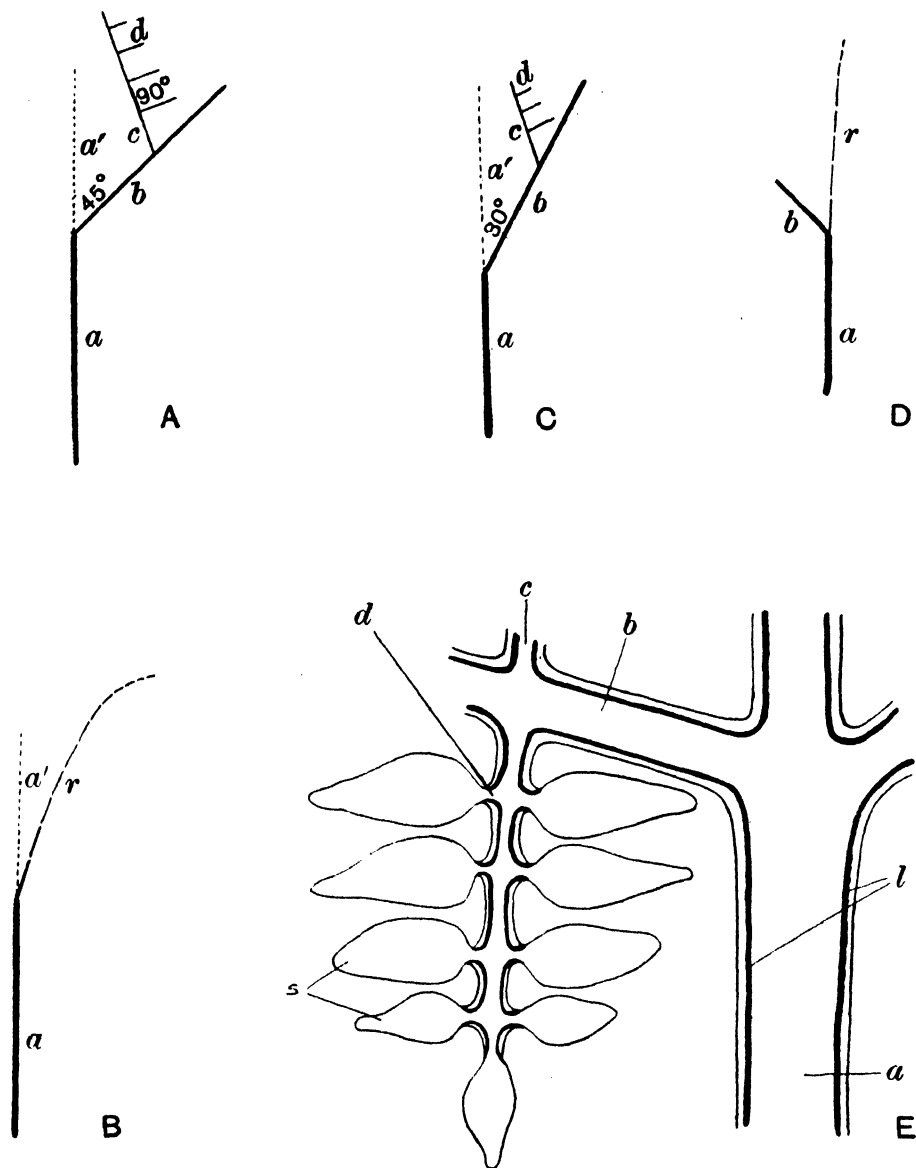


FIG. 5. Diagrams to explain the relations of the different parts of the fronds of *Pteridium aquilinum*. A, front view of frond from base of slope; B, side view of A, axis of first pinna not seen as it is in a plane at right angles to the paper; C, front view of frond from top of slope; D, side view of C; E, diagram to show arrangement of lateral lines (in the actual plant the branches are in different planes). *a*, petiole; *a'*, imaginary continuation of petiole; *b*, axis of first pinna; *c*, axis of pinnule; *d*, axis of subdivision of pinnule; *l*, lateral line; *r*, rachis of lamina; *s*, subdivisions of pinnules.

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which was probably not felt by the young developing fronds to nearly the same extent as in 1924.

In the sheltered valleys the surfaces of the pinnules are always placed more or less horizontal. The petiole (Fig. 5 *A*, *a*) up to the point of origin of the lamina is erect, and the stalks of all the pinnae (*b*) make an angle of something like 45° with it. The stalks (*c*) or midribs of the pinnules make an angle of 60° or more with the rachis of the pinna. These successive branchings are in different planes, but the ultimate subdivisions (*d*) of the pinnules all lie in the same plane and are usually arranged so that their midribs form approximate right-angles with the main axis of the pinnule (*c*). As the main rachis (Fig. 5 *B*, *r*) becomes more and more inclined, the angles above given will vary with each successive pair of pinnae. In all cases, however, the total effect is to present the pinnules so that the sun's rays at mid-day fall perpendicularly upon them. The lowest pair of pinnae of sheltered fronds are usually spread out to the left and right approximately in the same plane (cf. Pl. XXXVI).

In exposed specimens from the tops of the slopes the rachis, as already explained, is approximately vertical throughout, though occasionally the extreme tip may be slightly bent (Fig. 5 *D*). The stalks of the pinnae (Fig. 5 *C*, *b*) make a smaller angle (about 30°) with the petiole than in the sheltered specimens. The stalks (*c*) or midribs of the pinnules make an angle with the rachis of the pinna considerably less than 60° , while the subdivisions of the pinnules (*d*) form angles of about 80° with its main axis. In exposed specimens the lowest pair of pinnae are bent towards the adaxial side and form an acute angle with one another (cf. Fig. 5 *D*, *b* and Pl. XXXVI); in 1924 they were always situated on the side away from the wind, so that they exposed a small surface to the latter. These two pinnae stand out markedly from the rest which are borne on the flanks of the rachis, and are not bent towards the adaxial side. The pinnules in all parts of the exposed fronds lie approximately in the same plane as the pinnae and, as a consequence, stand more or less edge-wise so that the sun's rays do not fall perpendicularly upon their surfaces. They offer a very sharp contrast to the appearance of sheltered fronds. Usually the pinnules do not exhibit the extreme subdivision observable at the bases of the slopes.

There is little or no difference in the degree of hairiness of the pinnules. Those of exposed fronds have a tough texture and are coarse to the touch, whereas those of sheltered fronds are tender and succulent. The width of the sorus, as seen with a lens, is less in specimens from the tops than from the bases of the slopes. This agrees with Boodle's (1, p. 668) observations on leaves grown in a greenhouse and out of doors. The sori were ripe at the bases of the slopes on July 23rd, 1925, although unripe and greenish-yellow in colour at the tops.

The fronds of *Pteridium aquilinum* thus exhibit a decrease in height and size of all the parts with increasing exposure. Exposed specimens, moreover,

differ from sheltered ones in the far smaller inclination of the main rachis, in the bending of the lowest pair of pinnae towards the adaxial side, in the more acute angle between pinna and rachis, in the sub-vertical placing of the pinnules, and in their lesser subdivision.

(d) COMPARATIVE CONSIDERATION OF THE ANATOMICAL FEATURES OF THE PETIOLES IN SPECIMENS FROM HABITATS OF VARYING EXPOSURE.

The decrease in diameter of the petiole at ground level (Table II), as one passes up the slopes, corresponds to a decrease in the area of the cross-section at this point (Table VI). The area at the top of the petiole does not invariably show this constant gradation, for on the Erica-slope in 1922 the specimens taken from the middle of the slope had the smallest average cross-section. This may be compared with the fact that in 1924 the smallest fronds were found on the middle of this slope (Table II).

Table VI. *Comparison of areas of tissues in the base and top of the petiole of Pteridium aquilinum.*

(All observations recorded for three specimens cut in July of the respective years.)

| Position | Year | Base of petiole | | | | Top of petiole | | | |
|-----------------------------|--------|-----------------------------------|----------------|----------|-----------------|-----------------------------------|----------------|----------|-----------------|
| | | Area of cross-section in sq. cms. | % sclerenchyma | % steles | % ground tissue | Area of cross-section in sq. cms. | % sclerenchyma | % steles | % ground tissue |
| Erica-slope | Base | 1922 | 330.1 | 32.8 | 11.7 | 55.5 | 202.0 | 40.1 | 22.9 |
| | | 1924 | 321.7 | 32.3 | 15.2 | 52.5 | — | — | — |
| | Middle | 1922 | 259.9 | 40.1 | 9.9 | 50.0 | 97.8 | 47.2 | 25.2 |
| | | 1924 | 259.2 | 53.9 | 11.8 | 34.3 | — | — | — |
| | Top | 1922 | 175.7 | 51.9 | 12.5 | 35.6 | 108.3 | 46.0 | 26.1 |
| | | 1924 | 145.6 | 70.5 | 12.1 | 17.4 | — | — | — |
| Central Ridge | Base | 1922 | 335.0 | 34.9 | 16.3 | 48.8 | 239.1 | 54.5 | 23.0 |
| | | 1924 | 393.7 | 34.9 | 14.8 | 50.3 | — | — | — |
| | Middle | 1922 | 218.8 | 52.8 | 12.8 | 34.4 | 104.5 | 49.9 | 22.8 |
| | | 1924 | 201.1 | 48.0 | 10.8 | 41.2 | — | — | — |
| | Top | 1922 | 197.6 | 44.2 | 10.1 | 45.7 | 73.3 | 49.5 | 19.2 |
| | | 1924 | 133.6 | 49.6 | 10.6 | 39.8 | — | — | — |
| F 12 | Base | 1922 | 367.7 | 36.5 | 10.9 | 52.6 | 185.8 | 38.5 | 20.3 |
| | | 1924 | 321.9 | 36.6 | 9.9 | 53.5 | — | — | — |
| | Top | 1922 | 365.1 | 44.0 | 9.9 | 46.1 | 117.9 | 53.6 | 22.3 |
| | | 1924 | 229.4 | 47.3 | 11.8 | 40.9 | — | — | — |
| Junction of valleys A and B | 1922 | 563.8 | 25.6 | 13.7 | 60.7 | 349.7 | 30.1 | 18.0 | 51.9 |
| | 1924 | 841.7 | 28.3 | 11.9 | 59.8 | — | — | — | — |
| From near 12 | 1922 | 379.7 | 30.3 | 12.2 | 57.5 | 192.6 | 39.6 | 23.9 | 36.5 |
| | 1924 | 315.1 | 36.3 | 16.2 | 47.5 | — | — | — | — |
| Gravel in valley B | 1922 | 426.1 | 36.1 | 11.0 | 52.9 | 358.8 | 42.4 | 17.6 | 40.0 |
| | 1924 | 271.6 | 40.4 | 11.7 | 47.9 | — | — | — | — |

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The percentage of sclerenchyma (Table VI) at the base of the petiole, as a general rule, increases regularly with an increase of exposure, although there is a slight deviation at the top of the Central Ridge in 1922. The top of the petiole does not show the same uniformity. Thus, whilst in most cases the percentage of sclerenchyma is greater at the summits than at the bases of the slopes, an opposite result was obtained on the Central Ridge. The reason for this is not clear. A slight deviation was also noticed in specimens from the top and middle of the *Erica*-slope (cf. above). There is, however, a very marked difference between the percentage of sclerenchyma at the base and top of F 12, and when one compares the figures for the junction of valleys *A* and *B* (a sheltered spot) with those at the tops of the slopes, it is clear that there is ordinarily a marked increase of sclerenchyma accompanying an increase of exposure; in all probability this is to be related to the increased intensity of the wind.

Since the development of mechanical tissue will probably be related to the size of the frond, the ratio between the percentage of sclerenchyma and the height of the latter was determined for the different habitats (Table VIII). Even then, however, there is a markedly increased production of sclerenchyma as one passes up the slopes, despite the fact that the fronds are becoming progressively smaller.

The cell walls of the peripheral and central sclerenchyma (measured at the base of the petiole) increase in thickness without exception with increased exposure (Table VII). Similarly the thickness of the outer epidermal walls regularly increases as one passes up the slopes (Table VII). The similarity of the figures for 1922 and 1924 is striking.

In computing the vascular tissue the entire meristele up to and including the endodermis was measured. It was found impracticable to estimate xylem and phloem separately, nor did it appear that the latter varied at all appreciably in character or amount in the different habitats. The percentage of steles, whether at the base or at the top of the petiole (Table VI), does not vary in any regular manner in relation to exposure, which probably indicates that other factors are of greater importance. On the Central Ridge there is always a decrease in vascular tissue on the upper parts of the slopes, whilst the converse usually obtains on slopes facing south (*Erica*-slope and F 12). A relation to the water content of the soil is sometimes apparent (8, p. 57). Thus, the percentage of steles on the Central Ridge falls with the decreasing water-content of the soils. The low percentage at the base of the petiole in the middle of the *Erica*-slope, both in 1922 and 1924, corresponds to the lowest water-content. On F 12 slightly contradictory results were obtained in 1922 and 1924 (Table VI), but in either case the differences are not great; and in this connection it may be noted that the water-contents of the soils at the base and top of F 12 (the F 2 of Haines) do not differ appreciably (8, p. 57). It would seem, therefore, that the amount of vascular tissue produced is more

closely related to the water-contents of the soils than to the degree of exposure of the fronds.

Another factor which might affect the amount of vascular tissue, is the extent of the transpiring surface. With the object of investigating this, the ratio between the percentage of steles and the number of pinnae per frond was determined (cf. Table VIII). This ratio appears to have a more or less constant value according to the position of the fronds on the slopes. At the base and middle the ratio is 0.72-0.78, while at the tops it is greater, viz. 0.82-0.94. The ratio for the base of F 12 and for the junction of valleys *A* and *B* is considerably lower, which is not surprising seeing that these spots are very sheltered. The figures show a definite relation between the amount of vascular tissue and the extent of the transpiring surface, but they also indicate an increase in the former with greater exposure.

Table VII. *Comparison of the anatomical features of the base of the petiole of Pteridium aquilinum.*

(All observations recorded for July of the respective years; all measurements in μ ; 150 readings in each case.)

| Position | Year | Thickness of outer epi- dermal wall | Thickness of walls of sclerenchyma | Width of lumina of xylem elements |
|---------------------------|------|---|--|---|
| Erica-slope | | | | |
| Base | 1922 | 5.4 | 5.3 | 72 |
| | 1924 | 4.8 | 5.4 | 74.3 |
| Middle | 1922 | 7.3 | 6.5 | 60.6 |
| | 1924 | 7.4 | 7.7 | 61.4 |
| Top | 1922 | 7.7 | 7.0 | 55.8 |
| | 1924 | 8.6 | 8.5 | 55.8 |
| Central Ridge | | | | |
| Base | 1922 | 3.7 | 5.4 | 78.2 |
| | 1924 | 3.7 | 5.7 | 85.2 |
| Middle | 1922 | 4.7 | 6.3 | 52 |
| | 1924 | 4.7 | 6.4 | 55.8 |
| Top | 1922 | 5.7 | 6.5 | 52.2 |
| | 1924 | 6.4 | 7.2 | 45.6 |
| F 12 | | | | |
| Base | 1922 | 4.5 | 5.8 | 65.3 |
| | 1924 | 4.9 | 5.7 | 72.7 |
| Top | 1922 | 5.8 | 7.5 | 50.3 |
| | 1924 | 6.0 | 6.7 | 58.3 |
| Junction of valleys | 1922 | 3.9 | 4.7 | 67.8 |
| <i>A</i> and <i>B</i> | 1924 | 3.6 | 5.0 | 97.0 |
| From near 12 | 1922 | 3.9 | 5.1 | 72.7 |
| | 1924 | 3.4 | 5.7 | 82.4 |
| Gravel in valley <i>B</i> | 1922 | 5.7 | 6.9 | 62 |
| | 1924 | 6.3 | 7.0 | 63.7 |

The width of the lumina of the metaxylem tracheids decreases regularly with an increase in exposure. This indicates that, although exposure does not sensibly influence the amount of vascular tissue produced, it yet has an effect upon the water-conducting elements. Attention may again be drawn to the marked similarity of the figures in the two years (Table VII).

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The percentage of ground tissue (Table VI) diminishes with increased exposure, except that in 1922 the middle of the Central Ridge has the lowest percentage for the base of the petiole, while the percentage at the top of the petiole increases as one passes up the slope. The lateral lines occupied a similar position in all specimens and their anatomical features were not found to vary with the habitat.

Table VIII. *Ratios for certain anatomical features of Pteridium aquilinum.*

| Position | % sclerenchyma: Height of frond (base of petiole) | % steles: Number of pinnae per frond (base of petiole) | Thickness of xylem walls: Width of lumina of xylem (top of petiole) |
|---------------------------------|---|--|---|
| Erica-slope | | | |
| Base | 1.8 | 0.72 | 0.102 |
| Middle | 4.5 | 0.74 | 0.106 |
| Top | 4.2 | 0.93 | 0.110 |
| Central Ridge | | | |
| Base | 1.5 | 0.78 | 0.080 |
| Middle | 3.4 | 0.72 | 0.090 |
| Top | 3.6 | 0.82 | 0.110 |
| F 12 | | | |
| Base | 2.1 | 0.55 | 0.102 |
| Top | 3.2 | 0.84 | 0.108 |
| Junction of valleys A and B | 1.8 | 0.48 | — |
| From near 12 | 2.0 | 0.81 | — |
| From near gravel in valley B | 2.7 | 0.65 | — |

Table IX. *Comparison of petioles of Pteridium aquilinum in hollow and just outside,—Central Ridge.*

| (Measurements in μ .) | | | | | | |
|---------------------------|---|-------------------------------------|--------------------------|---|--|--|
| Position | Area of cross-section in sq. cm. 3 specimens | % scleren- chyma. 3 specimens | % steles. 3 specimens | Thickness of outer epidermal wall. 60 readings | Thickness of walls of scleren- chyma. 60 readings | Width of lumina of xylem elements. 60 readings |
| In hollow | 234.1 | 47.9 | 11.6 | 6.1 | 5.0 | 72.3 |
| Outside hollow | 220.6 | 49.1 | 10.9 | 6.9 | 6.0 | 65.7 |

Table X. *Comparison of petioles of Pteridium aquilinum from burnt and unburnt areas on the Erica-slope.*

| (Measurements in μ .) | | | | | | |
|---------------------------|---|-------------------------------------|--------------------------|---|--|--|
| Position | Area of cross-section in sq. cm. 3 specimens | % scleren- chyma. 3 specimens | % steles. 3 specimens | Thickness of outer epidermal wall. 60 readings | Thickness of walls of scleren- chyma. 60 readings | Width of lumina of xylem elements. 60 readings |
| Unburnt area | 198.7 | 53.3 | 13.8 | 8.6 | 5.9 | 68.8 |
| Burnt area | 145.6 | 66.3 | 12.1 | 7.0 | 8.5 | 55.8 |

That these anatomical differences in the petiole are in the main attributable to exposure, was in some measure confirmed by comparing bracken fronds from the inside of a hollow on the Central Ridge with others gathered from just outside. The latter showed a decided decrease in their cross-sectional area and in the percentage of vascular tissue, while they exhibited an increased

percentage of sclerenchyma, thicker epidermal and sclerenchyma walls, and xylem tracheids with smaller lumina (Table IX). Unfortunately measurements of the heights of these fronds were not made.

A further comparison was instituted between specimens from two adjacent areas, at about the same level on the Erica-slope, the one not recently burnt and covered with a more or less dense growth of the heath association (six years old), the other burnt in the previous autumn and therefore affording little or no shelter (Table X). In the exposed specimens there was again a decrease in the size of the petiole, the percentage of steles and the width of the xylem elements, together with an increase in the percentage of sclerenchyma and in the thickness of the outer epidermal and sclerenchyma walls.

(e) COMPARATIVE CONSIDERATION OF THE ANATOMICAL FEATURES OF THE PINNULES IN FRONDS FROM HABITATS OF VARYING EXPOSURE.

The thickness of the pinnules was measured in transverse sections at fixed intervals, viz. near but not at the mid-rib, half-way between the midrib and the margin, and close to the sorus, and an average of these measurements was taken (Table XI). The thickest pinnules are found at the tops of the slopes, which agrees with the naked-eye observation of their general texture (cf. p. 340). Specimens from the middle of the Central Ridge again show a discrepancy in 1922. The mass of sclerenchyma underlying the median vein was measured along a line bisecting the midrib, from the middle lamella of the adjacent endodermal cell to the *outer* wall of the epidermal cell¹. The depth of this sclerenchyma ridge increases progressively as one passes up the Erica-slope and F 12, but on the Central Ridge there is a decrease at the middle, while the base and top are practically the same (Table XI).

Exposed specimens frequently develop three rows of palisade cells, while in sheltered forms the palisade tissue is only one or two cells deep, the spongy tissue occupying the greater part of the mesophyll. The degree of development of the air-spaces also varies, but not so markedly as Woodhead (20, p. 369) found in his sun- and shade-forms. The air-spaces are fewer and of smaller dimensions on the tops of the slopes, the mesophyll being of a looser texture at the bases. The degree of forking of the veins does not appear to vary in the specimens examined.

For the comparative investigation of other anatomical features, transverse sections were cut half-way between the tip and the stalk of the pinnule next above the one used for determining the stomatal numbers. The average width of the hypoderm cells in these sections was measured from middle lamella to middle lamella in a tangential direction across the middle of the cell. Since only slight differences were observed, graphs were made from 300 readings

¹ The epidermis in this region has slightly thicker walls than elsewhere and it was therefore included with the mass of sclerenchyma.

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for each position on the slope (100 from each of 3 specimens). These (Fig. 6) show a clear increase in the widths of the hypoderm cells with an increase of exposure, but in all cases there is considerable overlapping. The maxima on the whole are better defined on the Central Ridge than on the Erica-slope, but the middle of this slope affords the most decided maximum of all. The marked similarity and overlapping of the graphs for the base and top of F 12 is in accord with the results previously obtained for specimens from this area (cf. Tables II-XI). It may be noted that the widths of the hypoderm cells exhibit a wider range at the top than at the bottom of the slopes.

Table XI. *Comparison of the anatomical features of the pinnules of Pteridium aquilinum in fronds from habitats of varying exposure.*

| (All measurements in μ .) | | | | | | | |
|-------------------------------|--------|--------------------------------------|--|---|---|--|---|
| Position | Year | Thickness of pinnule. 3 specimens | Depth of ridge of sclerenchyma on under surface of median vein. 3 specimens | No. of stomata per sq. mm. 60 readings | Widths of palisade cells. 150 readings | Lengths of palisade cells. 600 readings | Average volume of palisade cell (μ^3) |
| Erica-slope | Base | 1922 225.4 | — | 301 | — | — | — |
| | | 1924 218.0 | 163.1 | 353 | 15.6 | 47.3 | 9,079 |
| | Middle | 1922 242.5 | — | 291 | — | — | — |
| | | 1924 245.4 | 181.5 | 291 | — | — | — |
| | Top | 1922 253.0 | — | 276 | — | — | — |
| | | 1924 266 | 196.5 | 216 | 20.1 | 52.5 | 16,651 |
| Central Ridge | Base | 1922 270.9 | — | 291 | — | — | — |
| | | 1924 213.9 | 159.6 | 291 | 12.7 | 36.6 | 4,630 |
| | Middle | 1922 235.3 | — | 245 | — | — | — |
| | | 1924 222 | 146.2 | 228 | 17.5 | 49.8 | 11,809 |
| | Top | 1922 272.8 | — | 278 | — | — | — |
| | | 1924 234.6 | 159.1 | 208 | 18.1 | 53.2 | 12,717 |
| F 12 | Base | 1922 219.7 | — | 308 | — | — | — |
| | | 1924 212.2 | 182 | 287 | 15.1 | 39.5 | 6,983 |
| | Top | 1922 249.1 | — | 295 | — | — | — |
| | | 1924 249.7 | 222.1 | 251 | 18.3 | 51.1 | 13,425 |

In investigating the variations in the lengths of the palisade cells (Fig. 6), 600 readings were recorded for each position (200 for each of 3 specimens). In all cases, despite considerable overlapping, the longer palisade cells are at the tops of the slopes. On the Erica-slope there is little difference between the base and middle, and both on this slope and on the Central Ridge well defined maxima are only seen at the tops. The widths of the upper ends¹ of the palisade cells (Table XI) are appreciably greater on the tops of the slopes. The average volumes of the palisade cells, calculated from the average lengths and widths on the assumption that they are cylindrical, show a striking increase with increasing exposure at the tops of the slopes (Table XI).

¹ The palisade cells are practically the same width throughout and therefore measurement at the upper end only was deemed necessary.

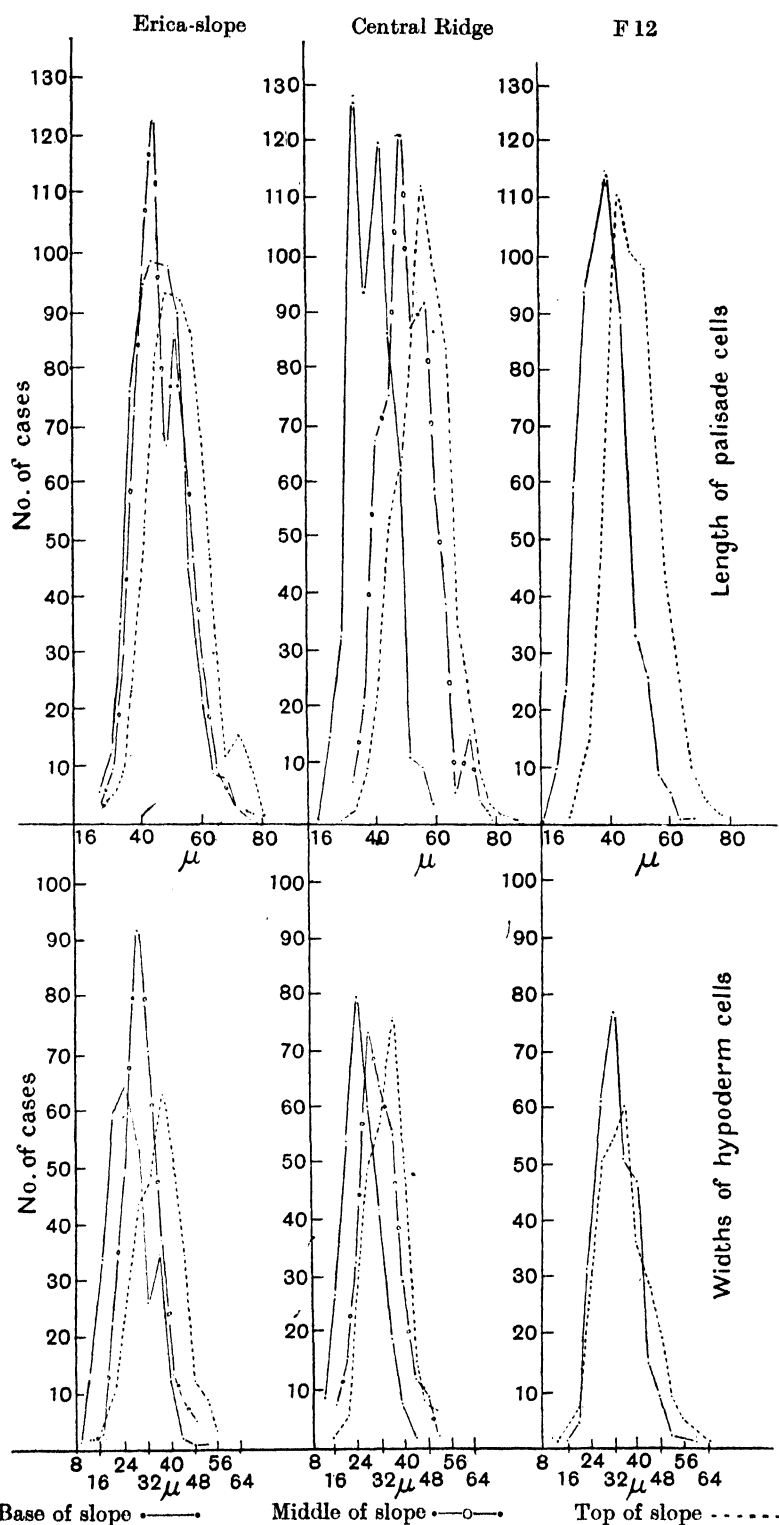


FIG. 6. Variation graphs showing (above) the lengths of the palisade cells and (below) the widths of the hypoderm cells in pinnules of *Pteridium aquilinum* taken from the base, middle, and tops of the slopes indicated. The two sets of graphs based on 600 and 300 measurements respectively.

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The number of stomata per square millimetre was estimated by means of a squared eye-piece, using the lowest pinnule furthest from the apex on a pinna situated about 7 cm. from the tip of the frond. There is a decided decrease in the number of stomata with an increase of exposure, as one passes up the slopes (Table XI). Other features of the stomata, such as their dimensions, the degree of elevation above the epidermis, and the size of the pore and respiratory cavity, do not appear to vary (1, p. 669).

Table XII. *Successive potometer readings with Pteridium aquilinum on F 12—base of slope, July 1925.*

| Time in secs. | Weather notes | Time in secs. | Weather notes |
|---------------|--------------------|---------------|---------------|
| 65 | | 97 | |
| 71 | | 93 | |
| 78 | | 83 | Breeze |
| 69 | | 100.4 | Less wind |
| 72 | | 114 | |
| 74 | | 121 | |
| 85 | | 113 | |
| 110 | Sunshine | 108 | |
| 116 | | 138 | Sunshine |
| 130 | Brilliant sunshine | 136 | |
| 99 | Sunshine | 110 | |
| 90 | Cloudy | 99.6 | Less sun |
| 91.4 | | 128.4 | Sunshine |
| 96.8 | | | |

Table XIII. *Average potometer readings (in seconds) for 1 hour taken simultaneously at two positions on the slope (Pteridium aquilinum).*

| Position | Time ... 10.45–11.45 | 12.25–1.25 | 3–4 | |
|---------------|----------------------|------------|-------|-------|
| Central Ridge | | | | |
| Base | 73.9 | — | 133.9 | — |
| Middle | 124 | 198.8 | 463.7 | — |
| Top | — | 165.8 | — | — |
| | Time ... 12–1 | 1–2 | 2–3 | 3–4 |
| Erica-slope | | | | |
| Base | 139.6 | — | 203.8 | — |
| Middle | 122.5 | 122.7 | 163.8 | 219.2 |
| Top | — | 450.6 | — | 503.7 |
| | Time ... 11.30–12.30 | 12.30–1.30 | | |
| F 12 | | | | |
| Base | 94.8 | 114.2 | — | — |
| Top | 61.7 | 141.9 | — | — |

Investigations with a Darwin potometer showed the transpiration check in *Pteridium aquilinum* to be very sensitive. The potometers were set up at different levels on the slopes, the fronds being placed at their normal height above ground level. The rate of absorption varied with extraordinary rapidity in response to small changes in wind-velocity or sun-intensity, a slight breeze or cloud increasing the rate of absorption, lack of wind or bright sunshine decreasing the rate (Table XII). The potometer readings also showed that during the morning on the Erica-slope and F 12 the rate of absorption was quicker at the middle and top than at the base of the respective slopes, whilst on the Central Ridge the rate was greater at the base than at the top (Table

XIII, cf. with Table I). In the afternoon the rates of absorption on all slopes were found to be slower than in the morning, the tops of the slopes having the slowest rates. The greater percentage humidity of the air at the tops than at the bases of the slopes (cf. p. 327) is no doubt in part responsible. The absorption data agree in a remarkable manner with those obtained for the evaporating power and percentage humidity of the air, and likewise show that the middles of the slopes do not always fall into line.

D. VACCINIUM MYRTILLUS.

(a) GENERAL MORPHOLOGY.

The Bilberry covers extensive areas on Hindhead Common, the plants clothing the ground where they occur to the practical exclusion of other members of the heath-association. The plants are usually small and densely branched, with an underground rhizome giving rise to a perennial overground stem system, the younger branches of which are green and assimilating. The alternate leaves have a broad base with decurrent edges, forming two longitudinal ridges situated almost on opposite sides of the stem and continued downwards through two or more internodes; the ridges are separated by concave furrows within which the stomata lie. The internodes are commonly more or less twisted. The leaves are borne on very short petioles, and have an almost erect lamina with a serrate margin.

(b) ANATOMY OF STEM.

The anatomical investigation was practically confined to the young green overground stem where marked anatomical differences were more to be expected than in the deciduous leaves. The subsequent description refers to cross-sections cut at a distance of $2\frac{1}{2}$ cm. from the apex of the main shoot, that is through the second or third internode. Such sections exhibit three to five prominent crests, corresponding to the longitudinal ridges above mentioned, and separated by furrows of varying depths.

The glabrous stem is bounded by an epidermis containing a few very small chloroplasts and provided with very thick outer walls in which cuticle, cuticularised layers and cellulose layers are easily distinguishable. Between adjacent cells the cuticle is deeply constricted (Fig. 7 A) and, at these points, the cuticularised layers likewise dip inwards forming slight pegs opposite the lateral walls. In the region of the ridges the cellulose layer increases in width. The cell-cavities usually appear square or tabular in cross-section and square or rectangular in longitudinal section, some being twice as long as broad; occasional cells appear polygonal in longitudinal sections. The different shapes are quite irregularly distributed.

The stomata are restricted to the furrows and arranged with their long axes parallel to that of the stem. The width of the stomatal zone varies with

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the depth of the furrows. When the latter are deep, the sides are often studded with stomata, but in the shallower furrows the latter are confined to a narrow median zone. The guard-cells, together with the subsidiary cells by which they are flanked (Fig. 7 *A* and *B*, *s.c.*), are sunk at the base of a broad shallow

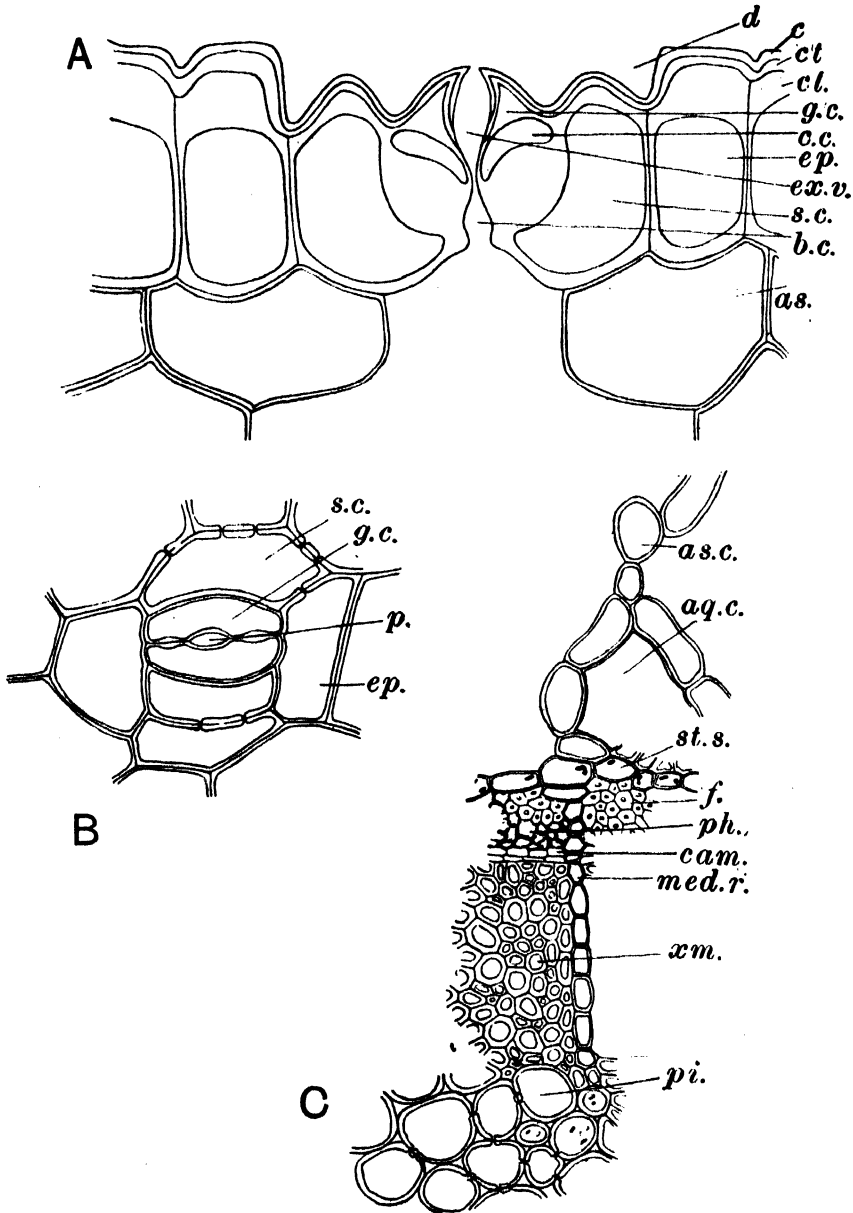


FIG. 7. *Vaccinium Myrtillus*, young stem. *A*, stoma and adjacent epidermis in transverse section; *B*, surface view of stoma and subsidiary cells; *C*, portion of stem in transverse section. *as.c.* assimilatory cells; *aq.c.* aqueous cells; *b.c.* back cavity; *c.* cuticle; *cam.* cambium; *c.c.* cell-cavity; *cl.* cellulose layer; *cl.* cuticularised layer; *d.* stomatal depression; *ep.* epidermis; *ex.v.* external vestibule; *f.* fibres; *g.c.* guard-cell; *med.r.* ray; *p.* pore; *ph.* phloem; *pi.* thick-walled pith; *s.c.* subsidiary cell; *st.s.* starch sheath; *xm.* xylem.

depression. The inner and outer walls of the guard-cells are very strongly thickened and together form more than three-quarters of the entire depth of the cell. In transverse section the outer walls are produced into prominent curved beaks enclosing an urn-shaped vestibule with a very narrow opening to the outside; this opening appears oval in surface view. Slighter projections from the inner walls give rise to a smaller back cavity (Fig. 7 *A*, *b.c.*). The actual lumen (*c.c.*) of the guard-cell, in transverse section, is a curved ellipse which tapers off in the neighbourhood of the pore. In surface view (Fig. 7 *B*) the guard cells are slightly elliptical. The subsidiary cells have large lumina (Fig. 7 *A*, *s.c.*) and resemble the adjacent epidermal cells though with far less strongly thickened outer walls. In surface view the subsidiary cells lie with their long axes parallel to those of the guard-cells (Fig. 7 *B*) and their lateral walls are seen to bear numerous simple pits.

Within the epidermis is a zone of compact assimilatory tissue with more or less isodiametric cells separated by small intercellular spaces and containing abundant chloroplasts (Fig. 8, *as.c.*) and only interrupted by the respiratory cavities below the stomata. In the same transverse section it ranges in depth between three and six layers of cells, but it also varies with the habitat, becoming deeper and more compact in exposed specimens although the surface area of the individual cells becomes smaller. Towards the interior the character of the assimilatory tissue gradually changes, the cells becoming irregular and the air spaces larger, so that the whole acquires a looser texture. In this inner region the cells are arranged in chains or irregular groups around large thin-walled empty-looking aqueous elements (Fig. 7 *C*, *aq.c.*), which either lie singly or form small groups separated by small intercellular spaces; on the same radius of the transverse section there are generally from two to four such groups separated by assimilating cells. There are no aqueous cells in the outer compact assimilating zone. The individual aqueous cells attain their maximum size midway between the latter and the starch sheath. In the mature condition they possess a very scanty protoplasmic lining and often harbour clustered crystals of oxalate of lime (Fig. 8 *D*, *cl.c.*).

In transverse sections of the growing tips of the stems the young aqueous cells appear as polygonal elements, rather larger than the neighbouring chlorenchyma cells and with less dense contents devoid of chloroplasts (Fig. 8 *A*, *aq.c.*). A very short distance below the tip they have enlarged to twice the size of the assimilating cells and are easily distinguishable (Fig. 8 *B*). This enlargement continues until the mature cells are from 2 to 16 times as big as the assimilating cells. In radial longitudinal sections through the growing point and the region just behind it, the aqueous cells are arranged in rough vertical files (Fig. 8 *C*), with the long axes of the cells placed transversely, successive files on the same radius being separated by vertical rows of assimilating cells. Further back this regular arrangement is not so apparent.

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Sections of wilted material mounted in paraffin oil show the aqueous cells contracted with their very thin walls thrown into numerous folds. If similar sections are mounted in water, however, the cells expand and resume a perfectly fresh appearance. It may therefore be concluded that these cells serve primarily for water storage. No mucilage was found in the contents.

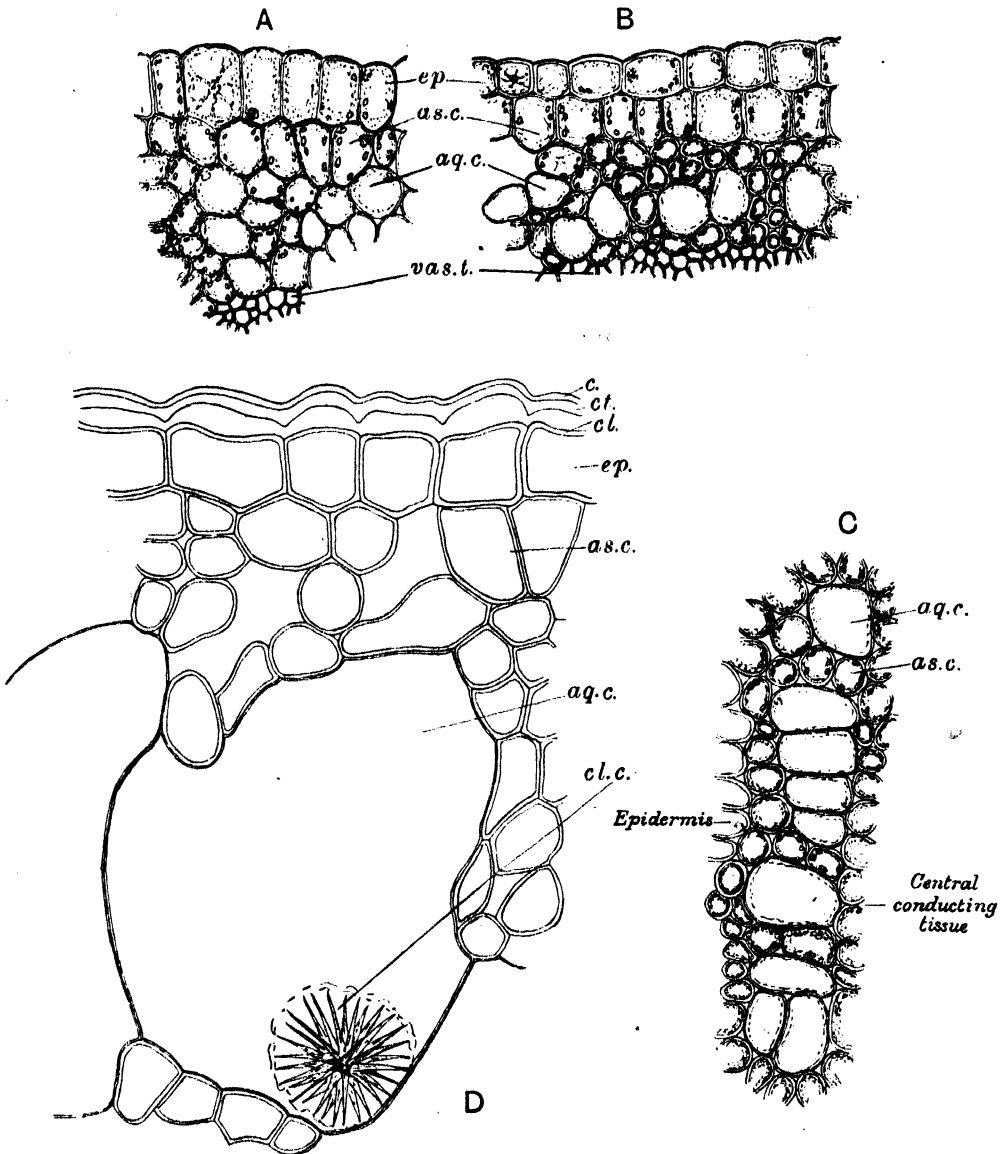


FIG. 8. *Vaccinium Myrtillus*, stem. A, transverse section of growing tip; B, transverse section a short distance behind growing tip; C, longitudinal section a short distance behind growing tip; D, transverse section of mature stem, cortical region. *a.s.c.* assimilatory cells; *aq.c.* aqueous cells; *c.* cuticle; *cl.* cellulose layer; *cl.c.* clustered crystal; *ct.* cuticularised layer; *ep.* epidermis; *vas.t.* vascular tissue.

fectly fresh appearance. It may therefore be concluded that these cells serve primarily for water storage. No mucilage was found in the contents.

The central region is bounded by a single-layered starch-sheath with tabular or polygonal cells which are rather larger than those on either side

(Fig. 7 C, *st.s.*) and include a few starch grains. In longitudinal sections the cells are rectangular, and roughly twice as long as broad. Immediately within this starch-sheath is a band of pericyclic fibres (*f.*), interrupted by the rays (*med.r.*) which are usually one cell, though occasionally two or three cells, wide and only two to four cells high. The pericyclic fibres are extremely long and narrow with white shining, stratified and lignified walls covered with simple pits. The ring of fibres is also broken where a leaf trace passes out, though the gap soon closes; the emerging petiolar strand has no fibres at all.

Secondary thickening sets in very early in the stem of *Vaccinium Myrtillus*, for the cambium is active in sections cut a very short distance behind the growing point and it has been impossible to recognise primary bundles. The elements of phloem and xylem are extremely small and those of the latter very thick-walled (*xm.*). The larger xylem-elements are very long, narrow vessels bearing bordered pits and provided with scalariform perforations, while the protoxylem has the usual spiral thickening. The wood-fibres are very long and narrow and bear bordered pits on all their walls. The ray cells are of the usual radially elongated type. The pith, which occupies from 2.7–8.9 per cent. of the cross-section, has polygonal cells with relatively thick cellulose walls which bear simple pits. In longitudinal sections the cells are rectangular, with their long axes transverse or longitudinal. In specimens gathered late in July and August the pith-cells are crowded with starch grains, but in early May there is little or no storage material in the pith.

(c) ANATOMY OF LEAF.

The leaves are dorsiventral with a single row of columnar palisade cells and a spongy tissue, usually about three cells deep and with large intercellular spaces, the cells forming a continuous layer above the lower epidermis except over the stomata.

The epidermal cells are tabular in transverse section, the cuticle being thicker in the upper than in the lower epidermis. Stomata were only found on the lower surface, although Woodhead (20, p. 388) states that in some forms a few occur in the upper epidermis. The Hindhead specimens agree with his moorland form.

(d) COMPARISON OF THE MORPHOLOGICAL FEATURES OF SPECIMENS FROM DIFFERENT HABITATS.

Since *Vaccinium* possesses a more restricted distribution on the common than *Pteridium*, specimens could not be obtained from all the habitats frequented by the latter. A particularly suitable habitat for comparative purposes was F 12.

In the first place, typical clumps of *Vaccinium* were selected at the base and top of the slope, the shoots were detached at ground level and the average length of 50 of the branches produced in the current season (1925) was

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measured in July. Those at the base of F 12 varied between 5·5 and 17·5 cms. in length, while those at the top varied between 1·5 and 8·5 cms.; the smaller range at the top is probably due to exposure. The average of the two sets of measurements (Table XIV) illustrates the marked decrease in height of *Vaccinium* at the top, and this fact is so obvious to the eye that it was considered unnecessary to repeat these measurements upon other slopes.

A cursory glance at the leaves of the two sets of specimens sufficed to indicate a marked difference between their respective surface-areas. The leaves on the current year's growth were therefore stripped off a number of the branches, and their outlines, including the short petiole, traced on a sheet of paper; with the help of a planimeter, the area of 50 leaves from each situation was thus determined. The surface area at the base of F 12 varied between 1·0 and 4·9 sq. cms. and at the top between 0·2 and 2·0 sq. cms.; these results recall those for the branches in the smaller range of the specimens from the top of the slope. The average of each set of measurements shows the striking contrast (cf. Table XIV) and similar differences are noticeable upon the other slopes.

Table XIV. *Measurements of Vaccinium Myrtillus.*

| (50 specimens in each case.) | | |
|------------------------------|--|--|
| Position | Average length of branches in cms. | Average surface area of leaves in sq. cms. |
| F 12 | | |
| Base | 9·4 | 2·8 |
| Top | 4·9 | 0·9 |

In 1925 and 1926 the *Vaccinium* plants growing on the summits were distinguished by the frequent reddish-yellow and sometimes intensely red colour of their leaves; in the valleys, on the other hand, the leaves were green, although a trace of the reddish-yellow colouring appeared here and there. The red colour is due to bright scarlet sap in the mesophyll cells, the intensity of coloration depending upon the number of cells involved. All the palisade cells may contain scarlet sap or some may be devoid of it. In the spongy tissue the coloured cells are fewer and more scattered, although they form a more or less continuous layer above the lower epidermis. In the leaves from the valleys only small numbers of these cells are found. This colouring matter, whose exact nature is not known, is also referred to by Woodhead, (20, p. 388).

Measurement of the angle between petiole and stem, on a number of slopes, showed no constant variation in relation to habitat. The measurements were, however, made only in July of 1925 and 1926, when the *Erica* and *Calluna* on the closing heath afforded considerable shelter. In view of the observations made on the bracken, it is possible that on newly burnt heath the angle of inclination of the leaf of *Vaccinium* would also be found to vary with the position upon the slope.

(e) COMPARISON OF THE ANATOMICAL FEATURES OF SPECIMENS
FROM DIFFERENT HABITATS.

Sections were invariably cut at a distance of $2\frac{1}{2}$ cms. from the tip of the current season's growth. In exposed plants the furrows were deeper than in sheltered forms. The area of the cross-section was always appreciably greater at the base than at the top of a slope. The percentage area of the cortex as a whole (i.e. aqueous + assimilatory cells), on the other hand, is slightly larger in exposed specimens. The assimilatory tissue¹, which makes up 40–50 per cent. of the entire cross-section, likewise shows an increase, except on the Central Ridge, where the specimens from the middle of the slope exhibit the maximum percentage of chlorenchyma (Table XV). The effect of exposure upon the development of the assimilating tissue is also brought out by comparing the base of the slope opposite the Erica-slope—a very sheltered spot where the percentage falls to 46.0, with the top of F 12—a very exposed region where it amounts to 49.8 per cent. The aqueous tissue varies between 26–33 per cent. and the relative area also increases slightly with an increase in exposure, the increase being most pronounced on the Central Ridge.

Table XV. *Comparison of areas of tissues, etc., in the young stem of Vaccinium Myrtillus from different habitats.*

(All observations based on average of three specimens collected in July 1924 from each habitat.)

| Position | Area of cross-section (sq. cms.) | % Aqueous cells | % Assimilating cells | % Fibres | % Xylem + Phloem | % Pith | No. of stomata per sq. mm. (165 measurements) |
|----------------------------|----------------------------------|-----------------|----------------------|----------|------------------|--------|---|
| Slope opposite Erica-slope | | | | | | | |
| Base | 247.8 | 30.65 | 45.0 | 2.9 | 14.2 | 6.4 | 287 |
| Top | 163.8 | 30.7 | 48.8 | 3.3 | 11.8 | 5.4 | 262 |
| Central Ridge | | | | | | | |
| Base | 234.1 | 26.6 | 48.9 | 2.6 | 15.8 | 6.1 | 224 |
| Middle | 156.4 | 27.9 | 51.0 | 3.7 | 13.0 | 4.4 | 249 |
| Top | 177.1 | 29.65 | 48.4 | 2.9 | 13.1 | 6.0 | 262 |
| F 12 | | | | | | | |
| Base | 214.9 | 32.9 | 48.8 | 1.6 | 11.1 | 5.6 | 203 |
| Top | 191.2 | 33.6 | 49.8 | 2.5 | 10.4 | 3.7 | 283 |

The pericyclic fibres are never strongly developed, but they show a marked relative increase at the tops of the slopes. The percentage of xylem and phloem clearly decreases as one passes up the slopes, a result in agreement with that obtained for *Pteridium aquilinum*. From 3.5 to 6.5 per cent. of the stem is occupied by pith, the area of which diminishes with increased exposure except on the Central Ridge where the top does not differ from the base (cf. however the middle).

In exposed positions there is thus an increase in the relative area of the cortex, and this increase is also exhibited by the aqueous tissue, assimilating

¹ In determining the percentage areas occupied by the tissues in the cortex the latter was roughly divided into groups of aqueous and assimilatory cells.

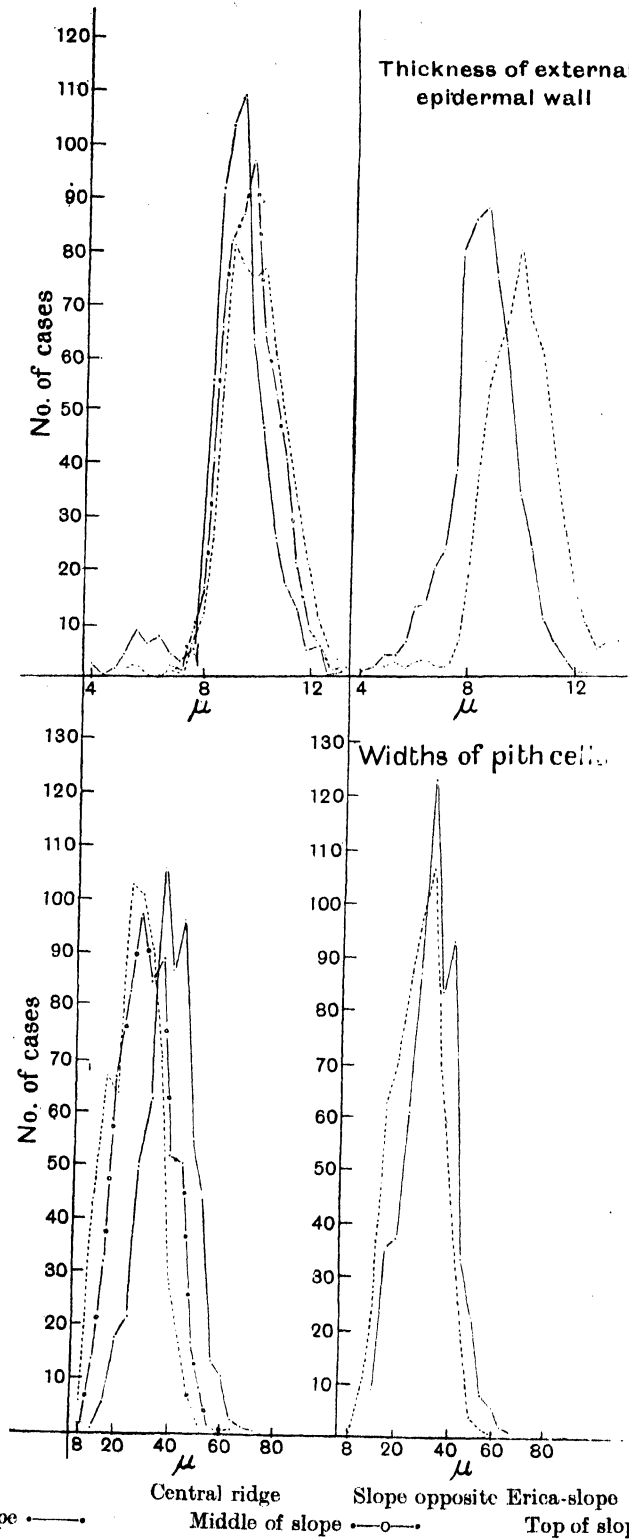


FIG. 9. *Vaccinium Myrtillus*, stem. Variation graphs showing (below) the widths of the pith cells, and (above) the thickness of the external epidermal wall at the base, middle, and top of two slopes. The graphs were each constructed from 600 measurements.

tissue, and fibres. On the other hand, there is a decrease in the percentage of vascular tissue and pith and a very decided decrease in the total area of the cross-section. There is plainly, however, some special factor affecting the growth of *Vaccinium* on the top of the Central Ridge, where the results as compared with those of the middle of the slope are often anomalous. The bracken is not affected to so marked an extent.

The graphs (Fig. 9) show an increase in the thickness of the external walls of the epidermis with increased exposure. The maximum for the base of the Central Ridge, exposed to the prevailing S.W. winds, lies at a higher value than that for the base of the Erica-slope. The external epidermal walls thicken over the crests of the ridges, which are the most exposed. The widths of the pith cells, measured from middle lamella to middle lamella, as seen in transverse section (Fig. 9), exhibit a decrease with increased exposure, and there is the same contrast for the slopes just mentioned. There is also a greater range of widths on the Central Ridge than on the Erica-slope.

The number of stomata per square millimetre in the furrows was counted in surface sections with the help of a squared eye-piece (Table XV), the sections being cut approximately $2\frac{1}{2}$ cms. from the tip of the stem. A decided decrease in stomatal numbers accompanies a decrease in exposure on the Central Ridge and F 12, which is directly opposite to results obtained for *Pteridium* on these slopes (cf. p. 348). There is no appreciable difference between the base and top of the other slope which is a sheltered one. Other features of the stomata, such as their dimensions, degree of depression below the general level of the epidermis, sizes of subsidiary cells, pore and respiratory cavity do not appear to vary.

E. MOLINIA COERULEA.

The Purple Heath Grass is conspicuous on certain parts of the common by reason of its magnificent tussocks. The more or less circular clumps bear numerous flat ribbon-like leaves which stand almost erect, while the tussocks of older specimens are well raised above the surface of the soil. Since Jefferies (9, p. 49) has given a full account of the morphology and anatomy of *Molinia coerulea*, no details need be given here.

(a) COMPARISON OF THE MORPHOLOGICAL FEATURES OF SPECIMENS FROM DIFFERENT HABITATS.

In the valleys the habit of this grass is very luxuriant, while towards the upper parts of the slopes it diminishes in size and abundance and, on the tops, is either altogether absent (Erica-slope and F 12) or exceedingly sparse and stunted. Little or no difference in the degree of hairiness of the different specimens can be detected.

There is a marked difference in the widths and heights of the tussocks according to their position upon the slope. The averages at the top of the

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Central Ridge are about half those at the base (Table XVI), and this is so apparent on all the slopes that further measurements were deemed unnecessary.

Table XVI. *Dimensions of tussocks of Molinia coerulea.*

| (Averages for ten specimens in cms.) | | |
|--------------------------------------|--------------------|-------------------|
| Position | Height of tussocks | Width of tussocks |
| Central Ridge | | |
| Base | 37.47 | 33.53 |
| Top | 29.3 | 17.45 |

It is not fully established however that the shortness of stature and generally limited growth on the tops are altogether the result of exposure. As their distribution in part suggests, the smaller plants on the upper levels may be new colonists endeavouring to secure a foothold for themselves, and in this case they are not directly comparable with the lower clumps. This can only be settled by observation over a period of years. There is, however, always a progressive decrease in size as one ascends the slopes, which suggests that the differences are in part certainly due to varying exposure.

On the top of the Central Ridge and other exposed situations on the common, the leaves are tightly inrolled, while at the sheltered bases of the slopes they are flat and inrolled only at the edges and extreme tips. According to Jefferies (9, p. 65) the leaf is normally spread out flat, but curls up in dry air, and the inrolling of the leaves of exposed plants on Hindhead Common is quite in accordance with this. The blades do not vary in position, being always practically vertical.

(b) COMPARISON OF THE ANATOMICAL FEATURES OF THE LEAF IN SPECIMENS FROM DIFFERENT HABITATS.

The leaf in transverse section has a smooth under surface, while the upper side is produced into a number of low ridges (Fig. 10 A), which are occupied by large vascular bundles (*v.b.*) enveloped in a band of sclerenchyma. The margins of the leaves are also provided with masses of fibres (*scl.*). The mesophyll is composed of small closely packed polygonal cells separated by small air-spaces. The epidermal cells are small and have strongly thickened walls, except in the furrows of the upper surface, where they are replaced by large relatively thin-walled motor cells. Stomata occur on both surfaces of the leaf.

In comparing the anatomical features of different specimens transverse sections were always cut at a distance of $2\frac{1}{2}$ cms. from the tip. The area of the cross-section (Table XVII) shows a very marked increase with increased exposure. The total thickness of assimilatory tissue (including lower epidermis) was measured in the furrows, from the middle lamella of the inner wall of the median hinge cell on the upper side to the extreme outer edge of the epidermis on the lower side. As in *Vaccinium Myrtillus*, the amount of assimilatory

tissue increases with increased exposure, although *Molinia* shows no such deviation upon the Central Ridge as was observed in the case of *Vaccinium* (cf. p. 355). The total thickness of the leaf at the ridges also increases as the exposure becomes greater (cf. *Pteridium aquilinum*, Table XI).

Table XVII. *Anatomical features of the leaf of Molinia coerulea.*

| Position | Area of cross-section of leaf (sq. cms.) | Thickness of assimilatory tissue in region of furrows (150 measurements) | Thickness of leaf at ridges (150 measurements) | Depth of hinge cells (150 measurements) | % Sclerenchyma at margins 3 specimens | No. of stomata per sq. mm. (75 measurements) |
|---------------|--|--|--|---|---------------------------------------|--|
| Erica-slope | | | | | | |
| Base | 23.6 | 39.4 | 128.5 | 37.4 | 3.8 | 796 |
| Middle | 39.0 | 43.8 | 134.5 | 38.6 | 5.6 | 831 |
| Central Ridge | | | | | | |
| Base | 28.0 | 42.6 | 123.5 | 34.5 | 2.9 | 838 |
| Middle | — | 55.9 | 163.0 | 41.6 | — | 765 |
| Top | 87.0 | 68.0 | 182.0 | 50.2 | 3.95 | 535 |

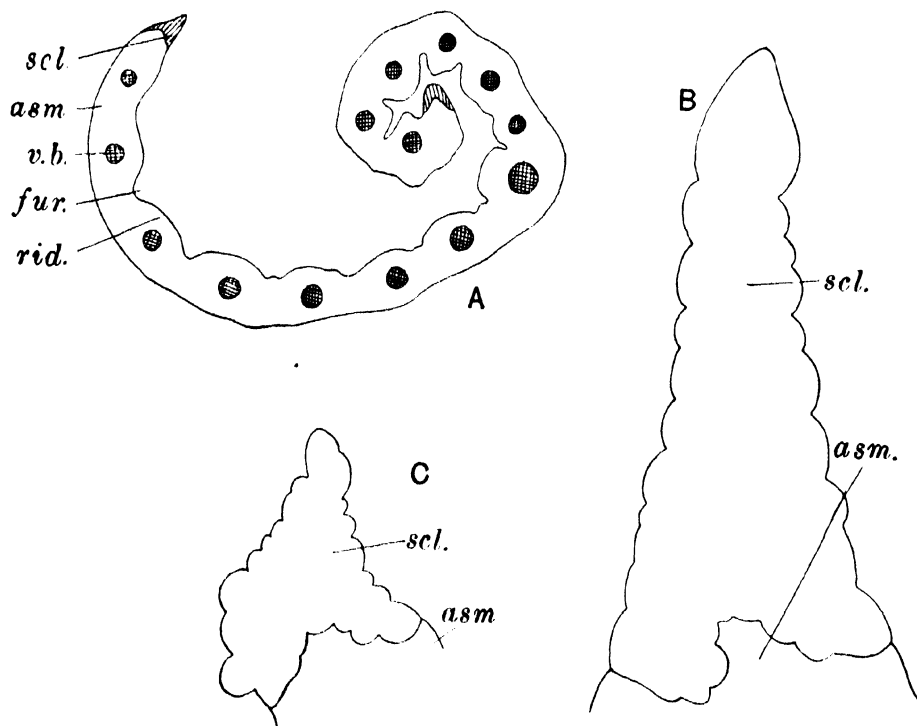


FIG. 10. *Molinia coerulea*, leaf. A, diagram of transverse section; B, marginal mass of sclerenchyma in transverse section from a blade taken from the top of the Central Ridge; C, the same, from a blade taken from the base of the Central Ridge, both enlarged to the same extent. *asm.* assimilatory cells; *fur.* furrow containing the motor cells; *rid.* ridge on upper surface of leaf; *scl.* marginal fibres; *v.b.* vascular bundle.

The numbers of stomata on the under surfaces of the leaves do not vary appreciably on the Erica-slope, but on the Central Ridge there is a decided decrease as one passes upwards (cf. *Pteridium aquilinum*, p. 348). The hinge

cells deepen (Table XVII) with increasing exposure, which corresponds to the tight inrolling of the leaves of exposed plants for the greater part of their length.

The masses of sclerenchyma at the margins of the leaf taper towards the outer edge, but, while sharp pointed edges characterise the leaves of exposed plants, those of sheltered plants have blunt edges. The percentage area occupied by this sclerenchyma in cross-section increases in exposed leaves (Table XVII and Fig. 10 *B, C*).

The size of the stomata and the thickness of the epidermal walls did not vary, and a study of the assimilating cells and air-spaces could not be undertaken.

F. SUMMARY AND DISCUSSION.

Specimens of *Pteridium aquilinum*, *Vaccinium Myrtillus* and *Molinia coerulea* have been collected from the valleys and from different heights on the slopes of Hindhead Common, Surrey, in order to determine the influence of varying degrees of exposure on the morphological and anatomical features of these plants. Data, which testify to the greater intensity of the wind and the greater evaporating power of the air on the upper levels of the slopes have been given in section B (pp. 324–328), where also the varying degree of exposure of the different habitats is considered. Transpiration will be more intensive on the upper levels, whilst the lower water-content of the soil (8, p. 39) will add to the stringency of the conditions to which the vegetation is subjected.

The general results of the investigation of the three plants as detailed in the preceding pages, are as follows. Emphasis must be laid on the fact that all the specimens examined were sun-forms. Increased exposure, as one passes up the slopes, is accompanied by a very marked and progressive decrease in the dimensions of all the plants examined. Not only is there a marked decrease in height, but in *Pteridium* there is a diminution in the diameter of the petiole and in *Molinia* in the width of the tussocks.

At the same time there is a reduction of the transpiring surface, which is accomplished in various ways. In *Pteridium* the laminae are obviously much smaller and are found to possess fewer pinnae, which are shorter, tougher, thicker, and less divided. In the case of *Vaccinium* the leaves of exposed specimens are smaller than those of sheltered ones and in *Molinia*, though the exposed leaves are wider, they are shorter than the others and moreover usually strongly inrolled. In *Pteridium* the angle of inclination of the rachis in exposed plants is considerably less than that in sheltered ones, so that the lamina is practically vertical; moreover, the pinnules are arranged more or less edgewise by comparison with their horizontal arrangement in the valleys. The lowest and longest pair of pinnae are bent towards the adaxial side and form an acute angle with one another in the exposed fronds of the bracken, and in 1924, when owing to the recent fire there was very scanty protection from surrounding vegetation, these pinnae were always situated on the side of the

frond away from the wind, thus reducing the transpiring surface exposed to the latter. No variation in the hairiness of the different plants was noticed which is not remarkable since only sun-forms were examined. The exposed sori of *Pteridium* are narrower than those on the sheltered fronds, and ripen later, a fact which testifies to the more severe conditions at the tops of the slopes.

Skipper (15, pp. 49, 50), comparing different branches of *Ulex nanus*, found that the leaves on the exposed branches were considerably larger than those on the sheltered ones. This is contrary to the results here obtained, and may indicate a different response on the part of the evergreen; it must be remembered, however, that Skipper compared leaves from different parts of the same plant.

The leaves of exposed plants of *Vaccinium* produce a red pigment in the mesophyll. According to Kerner (11, p. 231) and Overton (12, p. 171), such a coloration may be produced by intense cold or strong illumination. It has also been shown to be a means of increasing the temperature of the leaves (16, p. 137). The abundant production of such red pigment by exposed plants of *Vaccinium Myrtillus* may well be related to the extreme conditions to which they are subjected.

The thickness of the outer epidermal walls, including the cuticle, increases with increased exposure (cf. Skipper, 15, pp. 49, 50, Grevillius, 7, p. 44). This is particularly evident in the stem of *Vaccinium* where the epidermal walls thicken on the crests of the ridges which are the most exposed parts.

No appreciable differences in size or position of the stomata with reference to the other epidermal cells was noticed in the various habitat-forms. In *Pteridium aquilinum* the stomata were always raised, while in *Vaccinium Myrtillus* they were always markedly depressed and in *Molinia coerulea* level with the epidermis. Whilst in the bracken no differences in the degree of exposure of the stomatal apparatus could be recognised in different specimens, the exposed stems of the Bilberry have deeper furrows and the stomata are thus less exposed. In *Molinia* the motor cells are larger in the exposed leaves which probably corresponds to the latter being usually strongly inrolled.

Fewer stomata are usually found in exposed than in sheltered plants, but this was not the case in *Vaccinium Myrtillus*. Grevillius (7, p. 48), in comparing exposed plants in a dry rocky treeless plain with normal forms, found that the stomata of the former were more closely crowded. Keller (10, p. 224) likewise observed an increase in the number of stomata in exposed leaves of steppe plants, and Yapp (21, pp. 826–28) and Rea (13, p. 56) an increase in the number of stomata on the upper and more exposed leaves of *Spiraea Ulmaria* and *Campanula rotundifolia* respectively. Skipper (15, pp. 49, 50) likewise in dealing with *Ulex nanus* found an increase in the number of stomata in exposed leaves. These varying results indicate that the number of stomata is perhaps dependent on a multiplicity of factors, although in the heath plants

here considered it frequently decreases with increasing exposure¹. Attention may be drawn to the fact that the numbers of stomata per unit area in *Molinia* are two to three times as great as in either of the other plants and, as they occur on both sides of the leaf, this plant probably has great powers of transpiration when circumstances admit of it (9, p. 71).

Water-storage tissue is only developed in *Vaccinium* where it shows a relative increase in amount in exposed specimens. While the extent of development of a hypoderm in the pinnules of *Pteridium* does not appear to be determined by the degree of exposure, yet, when present, the hypodermal cells of exposed plants are wider than those of sheltered specimens.

Despite the decrease in leaf-area and in the height and width of the petiole or stem as the case may be, there is usually a very marked increase in the percentage amount of strengthening tissue produced in all parts of the over-ground system. At the same time, in *Pteridium* there is an increase in the thickness of the walls of the component elements. These features are no doubt related to the more powerful wind at the summits. The percentage of ground tissue is usually in inverse ratio to that of sclerenchyma, so that it exhibits a decrease in exposed plants. Since this is often the region of food-storage, its reduction implies reduced activities also in that direction.

The vascular tissue shows a clear tendency to decrease in amount with increased exposure, both in *Pteridium* and *Vaccinium*, but it would seem that this feature is also related to the water-content of the soil (cf. pp. 342, 355). In *Pteridium*, where this point was alone investigated, there is a very marked decrease in the width of the xylem tracheids with increased exposure.

The thickness of the leaves increases with increased exposure and this is largely due to the presence of a greater volume of assimilatory tissue (cf. 1, p. 662; 7, p. 54). In *Pteridium* the exposed pinnules produce more layers of palisade than the sheltered ones, whilst in *Vaccinium* there is usually an increased amount of assimilatory tissue in the stem; in the leaf of *Molinia* the difference is very striking (cf. Table XVII). In *Pteridium*, the only form investigated from this point of view, there is a marked increase in all dimensions of the palisade cells in the exposed pinnules, a result in agreement with that obtained by Skipper (15, p. 50) for exposed branches of *Ulex nanus*. In the latter case, however, the increased length of the palisade cells is accompanied by an increase in leaf-area which is not true of the bracken, facts which show that the enlargement of the assimilating tissue is not necessarily a compensation for reduced leaf-area. The assimilating tissue was always more compact in the exposed specimens as a result of a reduction in the size of the air-spaces.

Where measurements have been made on specimens from the same habitat in successive years, there is often a striking similarity between the figures (cf. Tables, II, VI, VII, XI). In fact the variations between successive yearly

¹ Cf. also Salisbury, *Phil. Trans. Roy. Soc. B*, cccvi, 1927, p. 1.

measurements are not uncommonly quite insignificant in comparison to the differences between the measurements of specimens collected on the same day, but from different levels on the slopes. These facts testify not only to the general uniformity of the conditions at the same spot year after year, but also to the marked difference between conditions of existence in the different habitats here considered.

Nevertheless, the differences that occur between the 1922 and 1924 figures in the tables cited are generally, and especially on the middles and tops of the slopes, quite in agreement (in their direction of change) with what would be expected from the increased exposure obtaining on the areas in question in 1924 (cf. p. 325). It may also be noticed that the figures for the tops in any one year not uncommonly agree to some extent with the relative degrees of exposure of the tops of the different slopes mentioned on p. 324.

As regards the specimens of *Pteridium* collected at the junction of valleys *A* and *B*, where very considerable shelter is found (cf. p. 325), the data obtained from them nearly always fall into line with the conclusions above outlined. Thus they afford the tallest fronds with the most massive petioles, and the smallest percentage of sclerenchyma. The specimens near 12 should be compared with those from the middles or tops of the other slopes. It will be found, however, that the figures relating to them are in general much more like those obtained for specimens from the valleys, which no doubt corresponds to the fact that at 12 there was very considerable shelter, owing to the height and density of the heath vegetation, and a very rich soil. The specimens from the gravel in valley *B* frequently have very sturdy petioles, but otherwise resemble plants from the middles of the slopes. Comparing the three sets of specimens with one another it may be noted that the bases of the petioles of the sheltered forms show a larger area of cross-section, smaller percentage of sclerenchyma, larger percentage of steles, and more ground tissue than the more exposed fronds on the gravel. The tops of the petioles do not afford such clear data.

The general result of these observations is thus to show a marked and progressive variation in external and internal features of the plants examined in response to increasing exposure, and a further confirmation of this conclusion was obtained by comparing specimens of *Pteridium aquilinum* growing side by side and yet with different exposure. Two such cases are fully considered on pp. 344-345.

It is, however, altogether impossible to separate the effects of exposure from the possible influence of water-content and other variable features of the soil. Wherever there is good shelter on Hindhead Common, there is a relatively high water- and humus-content, and these factors no doubt materially affect the development of the plants or of certain of their characteristics. Data are given on pp. 342, 343 which indicate that the development of the vascular tissue in the bracken may be more directly related to soil water-

content than to other factors. Possibly some of the exceptional results noted are to be ascribed to the influence of soil-factors. Some of the most marked divergences from the general rule were observed in the middle of the Central Ridge in 1922. The bracken fronds here exhibited thinner petioles, a larger percentage of sclerenchyma, a smaller percentage of ground tissue, and a smaller number of stomata per unit area of leaf surface than either at the bottom or top of the slope. This is possibly related to the fact that the middle of this slope in 1922 showed a lower water-content, both at 2 and 9 in. depths, than at the bottom or top (8, p. 38). The ground however exhibited a good many bare patches, so that the *Pteridium* was possibly more exposed to the wind than at the base and top of the slope. In this connection it may be noted that the middle of the Central Ridge also gave some anomalous results in 1924 (Table VI), for which year no soil-data are available. The middle of the Erica-slope, too, in a few cases (Tables II, VI) did not fall into line with the bottom and top, and this again accords with soil-data obtained in 1922 (8, p. 57). It may well be that at the middle of the slopes special conditions (e.g. wind currents) obtain which it is at present impossible to analyse.

From the preceding survey it can be gathered that the modifications brought about by increased exposure are such as will tend to decrease transpiration, conserve the water supply of the plant, provide additional mechanical tissue, and increase photosynthesis. These are just the changes that have frequently been observed when a comparison has been made between the features of sun- and shade-leaves (19, pp. 18-21). Thus, increased thickness of the epidermal walls and thicker leaves harbouring a greater volume of chlorenchyma with fewer air-spaces have been noted in sun-leaves as compared with shade-leaves by Woodhead (20, p. 398), Skipper (15, p. 34), and Boodle (1, p. 663). Stober (17, p. 89) noted the same differences in comparing the winter with the summer leaves of various plants. Boodle (1, p. 663) records the occurrence of more hypoderm in the sun-leaves of the bracken. Skipper (15, p. 37) found that the stem of the shade form of *Ulex europaeus* has a smaller total proportion of xylem and sclerenchyma, and a larger pith than that of the sun-form. The leaves are placed at a wider angle in the former than in the latter. On the other hand, the area of the sun-leaves was found to be greater than that of the shade-leaves (15, p. 22), a result harmonising with that obtained by comparison of exposed and sheltered leaves of *Ulex nanus*, but contrary to my own results (cf. p. 360).

The stomata of the heath plants examined mostly decrease in number with increased exposure, but exhibit no variation in size. This decrease in number of the stomata is noted also by Stober (17, p. 89) in winter-leaves and by Boodle (1, p. 663) and Woodhead (20, p. 398) in sun-leaves, although the latter found that in some cases there was an increase. Skipper (15, p. 34) observed such an increase in the sun-leaves of *Ulex europaeus* and in exposed leaves of *Ulex nanus*, but this was accompanied by a decrease in the size,

and a marked increase in the depth of the vestibule. It seems possible that the direction of alteration in numbers of stomata as between sheltered and exposed forms may depend to some extent on whether changes take place in the stomata themselves. Delf (2, pp. 436-7), in considering the behaviour of stomata in halophytes, came to the conclusion that their distribution is a variable feature, not influenced by habitat or transpiration (cf. also 14).

In view of the general resemblance between exposed plants and sun-forms on the one hand and sheltered plants and shade-forms on the other hand, as brought out by the present investigation, and bearing in mind that all the specimens here examined were growing in full sun, it can only be agreed that the results altogether support Boodle's view that "the amount of illumination is not the only factor determining the structure of the leaf."

I take this opportunity of expressing my thanks to Prof. F. E. Fritsch for his helpful criticism and advice. My thanks are also due to Miss G. Foreman, B.Sc., Miss E. Buglear, B.Sc., for help in field work; and to Dr F. M. Haines.

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WARBURTON MOSS: A STUDY OF CERTAIN SEMI-NATURAL PLANT COMMUNITIES IN NORTH-EAST CHESHIRE

BY E. PRICE EVANS.

(With Plates XXXVII and XXXVIII and two Sketch-maps in the Text.)

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INTRODUCTION.

LIKE the Cheshire Plain in general the part under consideration here affords little scope for the study of purely natural plant communities: in such highly cultivated areas the field worker is drawn towards the study of semi-natural communities, that is, all grades between the natural and the purely artificial in which "the vegetation is itself spontaneous, i.e. has occupied the ground without the aid of direct human action, but has nevertheless been partly determined or markedly modified by man or his animals. . . . Vegetation which owes its existing form to human activity, though not actually sown or planted by man, shows the same classes of units as purely natural vegetation, and can be treated just in the same way. The human activity in question—burning, pasturing, mowing, etc.—has to be taken as one of the constant factors of the habitat—indeed, as the differentiating or *master factor*¹."

¹ A. G. Tansley, *Practical Plant Ecology*, pp. 21, 42.

An attempt may now be made to give, in outline, the results of observational and experimental studies, undertaken during the five years 1923–7, on the general flora of a part of Warburton Moss and in particular on the weed-flora of arable land in the three districts—Warburton, Rostherne, and Castle Mills [Map 1 A, B, C, respectively]—situated within a radius of about five miles of the town of Altrincham, Cheshire. These areas were selected for this work because they afford an opportunity for the study of plant-communities on very different types of soil—on the acid peat of the lowland moss and on the less acid but silty peat of the moss-margin, on the light, silty, sandy, gravelly or medium loamy soil of the river terraces, and on the light, medium, heavy, and very heavy loams of the glacial and fluvio-glacial deposits.

The study of the geology of the Cheshire Plain from the “solid” map is apt to be misleading, for it throws little light on the existing surface of the plain: the Triassic rocks of this map are overlain, almost everywhere, by much younger deposits and, speaking generally, are much too deeply buried to have any direct influence on the vegetation. At the same time it must be borne in mind that some of the superficial deposits, notably those of glacial origin, were derived in part from the Red Rocks¹ and also that in certain localities, the Red Keuper Marls, the uppermost layer of the Triassic series, have been used for the amelioration of the arable land through the process of marling. Still, the fertility of the soil of Cheshire must be attributed very largely to the composite nature of the glacial and fluvio-glacial deposits, and to a smaller extent to the river terrace formations and the sedentary deposits that have developed upon them.

The bed rocks. Despite repeated crustal movements of elevation and depression, the area covered by the plain to-day has persisted from remote geological times as a depression relative to the surrounding areas²: through a very long period the Cheshire Plain has been a repository for the material denuded from the surrounding upland regions and for the material transported from the more distant areas. On the floor of the depression, resting on very ancient strata, are rocks of Carboniferous age; resting on them are rocks which, collectively, may be termed New Red Sandstones. Except in a few places where the Red Rocks actually crop out, the whole plain is further covered with deposits of glacial or post-glacial origin.

The economic products, coal and salt, belong to the first and second of these series of rocks respectively, and they form the bases of the industrial wealth of this part of the country; the chief economic product of the covering deposits is soil—fertile soil which is the basis of the agricultural wealth of the Cheshire Plain.

The glacial and fluvio-glacial deposits. During the Ice Age the Red Sandstone Plain was invaded by an ice-sheet, which at the maximum of glaciation

¹ Rastall, 1916; Kendall and Wroot, 1924.

² Jones, 1924.

covered the whole basin and impinged on the flanks of the surrounding uplands; as the climate ameliorated this ice-sheet retreated through the gap in the north-west whence most of it had come. Till or Boulder Clay—the ground-moraine of the ice-sheet—was left behind strewn over the surface, obscuring but not wholly obliterating its pre-glacial features. From an examination of some of these deposits it seems certain that water played an important part in their deposition: during the gradual retreat of the ice-sheet—perhaps with fluctuating advance and retreat—the glacial or ice-born streams sorted and re-sorted the glacial clays, silts, and sands, and it is probable that some of these deposits were laid down in lakes held between the ice-sheet and the elevated areas¹.

In the higher parts of the plain the surface deposits—mostly glacial clays², silts, and sands—are much the same to-day as they were at the close of the glacial epoch. In some of the lower parts they are rather different; for there are to be found series of deposits or relics of deposits which were laid down during the changes of sea-level or of climate or both that occurred between the close of that epoch and the present day.

It is probable that some time during the Ice Age the drainage of the Cheshire Plain was southwards into the Trent and the Severn systems; on the dissolution of the ice the northerly drainage was re-established. The swollen ice-born streams ploughed their way through the glacial deposits re-excavating their old valleys but sometimes also forming new courses.

The river terraces. At the present day certain deposits known as river terraces on the flanks of these valleys show that periods of excavation alternated with periods of deposition. The amelioration of the climate from the immediate post-Glacial period—the Steppe period—may have released material which would be carried away by the rivers to be deposited on the flood-plains at lower levels. In the case of the Mersey, the highest of these flood-plains, known as the High Terrace (because of its position with respect to other terraces and the present river-level, not because it has any great absolute altitude), may have been formed when the river was much larger than it is to-day. However that may be, there remain extensive deposits belonging to this first ancient flood-plain on the flanks of the Mersey in north-east Cheshire showing that the river meandered at one period over a flood-plain about seven miles in width; and in parts of the valley between the high terrace and the modern alluvial flood-plains, which are variously termed *eas*, *ees*, or *eyes*, are other transported deposits of the nature of river terraces which from their position may be termed Middle Terraces.

The mosses and submerged forests. In depressions in the High Terrace or between this terrace and the flanking glacial deposits lie those characteristic

¹ Pocock, 1906.

² The term "glacial clay" has been used throughout this paper (and on the map) for clay of glacial or fluvio-glacial origin: most of this clay, but not all of it, is typical Boulder Clay.

features of this part of the country—the lowland mosses. The formation of these peat-bogs was probably initiated during the closing stages in the existence of lakes which occupied the western apical water-logged portion of what has been termed the Manchester Plain¹.

At the mouth of the Mersey and under its coastal strands and marshes are alternate layers of peaty and sedimentary deposits which, collectively, may be termed Submerged Forests.

Time relations and correlations. The history of this area during the closing stages of the Glacial period and onward to the present day must be interpreted in the light of the study of the river terrace deposits, the peat-mosses, the moss-margins with their alternate layers of peat, silt and silty peat, and the submerged forests, correlated with the study of seemingly related features in the adjoining parts of this country and in the low-lying parts of Fenno-Scandinavia. These deposits are all indications of geological changes which may eventually be definitely correlated with the movements associated with the raised beaches and the submerged forests of some parts of the coasts of the British Isles and with the deposits of the Yoldia Sea, the Ancylus Lake, and the Littorina Sea of Fenno-Scandinavian post-Glacial history.

There are good reasons for believing that the last great movement that affected this area—a movement that caused the final submergence of the Great Forests—occurred towards the close of the Neolithic period in Britain²: in point of time this would probably be equivalent to the early stages of the Littorina Sea. The events that led to the formation of the High Terrace, to the beginning of the growth of the Mosses³, and to the formation of the Middle Terraces precede this movement in time, and some at least of these deposits may eventually be definitely correlated with those of the Yoldia Sea and the Ancylus Lake.

Post-Glacial time has been divided into climatic periods as follows: Arctic and sub-Arctic, Boreal, Atlantic, sub-Boreal and sub-Atlantic⁴.

The Boreal period corresponds to the Ancylus stage of the Baltic and within this continental epoch the epi-Palaeolithic (Mas d'Azil-Tardenois) period probably occurs. The Atlantic period corresponds to the Littorina stage of the Baltic and within this moist epoch the Neolithic period probably begins. The sub-Boreal division of post-Atlantic time includes the late Neolithic and Bronze Ages: the sub-Atlantic includes the Iron Age.

The Boreal and early Atlantic deposits are estimated to have been laid down from about 6500 to about 9500 years ago; the pre-Boreal more than 9500 years ago. The Atlantic period probably lasted about 3000 years (c. 5200 B.C. to 2200 B.C.); the sub-Boreal from 2200 B.C. to about 800 B.C.; and the sub-Atlantic from 800 B.C. to historic times⁵.

¹ Jones, 1924.

² *Ibid.* 1924.

³ "To the steppe period we must attribute the beginning of our peat deposits." Kendall and Wroot, 1924.

⁴ According to Blytt and Sernander.

⁵ According to the geo-chronology of Gerard de Geer.

Palaeo-botanical evidence. (a) In Scandinavia as the outcome of a micro-palaeontological study of the different horizons in the peat-bogs of that country a more or less complete succession has been established. After the retreat of the ice-sheet an arctic flora invaded the country from the south-west: this flora occupied the land till the later stages of the Yoldia Sea when the birch arrived, forming the first woods in Scandinavia. Early in Ancyclus times the pine arrived and may be said to have been the dominant tree throughout the Ancyclus Lake period. Towards the end of that period the oak entered the country and oak-woods became dominant from that time well into Littorina times. The last of this important series of forest-making trees to arrive was the beech, remains of which may be found (though sparingly) in the upper layers of the peat-bogs¹.

(b) In the British Isles it seems that the plant succession in post-Glacial times followed the lines of that in S.W. Sweden, except that pine, though present in quantity, was never dominant to the same extent as on the continent. This is a conclusion that may safely be drawn from the pollen-diagrams of those peat-bogs and mosses in this country that have already been investigated along the lines suggested by Erdtman².

The first dominant tree was birch, accompanied very soon by a great abundance of hazel, and followed by pine and willow; then came elm and oak, followed by alder, then lime; and finally hornbeam and beech³. The pollen-diagrams also show that after the immigration of the alder the pine rapidly diminished in number and either disappeared or became very scanty in late Boreal and early Atlantic times. It was never so abundant as on the continent, the continental "pine period" being, in Great Britain, mainly a "birch period."

From a study of the pollen-spectra of the basal layers of some of these peaty deposits, two important conclusions—important at least as far as the history of this area is concerned—may be drawn: the Leasowe Submerged Forest (Upper Forest) of Cheshire is fairly contemporaneous with the base of the Pennine peat and with the base of the mosses on the 25-foot beach of Wigtownshire, which were formed during the Atlantic period⁴; and the base layers of one of the mosses of the Lancashire-Cheshire Plain (Chat Moss) show the characteristics of deposits (great abundance of birch and hazel) which were formed at least as early as the Boreal period⁵.

¹ Wright, 1914.

² Erdtman, 1924.

³ *Ibid.* 1926.

⁴ Woodhead and Erdtman, 1926.

⁵ In correlating the climatic periods of the British Isles with those of Scandinavia care must be taken to give due consideration to the position of the islands with respect to the land mass on the one hand and to the cyclonic depressions of the Atlantic on the other. Thus, during the Boreal period the south-east of England resembled Scandinavia with its dry continental climate; the west of the islands was probably much damper and peat-bogs were being formed.

THE ALTRINCHAM LOCAL AREA.

Politically, the area covered by the map (Map 1) belongs to Cheshire; but physically it belongs partly to the Cheshire Plain and partly to the Manchester Plain: the 100 ft. contour line, which has a general east and west trend, forms a rough boundary between the physical divisions.

Deposits of glacial or of fluvio-glacial origin overlie the Red Rocks in the southern half of the area; but in the northern half these in their turn are overlain by other deposits, some of river terrace and yet others of moss-formation.

Such a diversity of deposits yields a great variety of soil, ranging from the stiff clayey loams of the glacial and fluvio-glacial clays, through the medium soils of the glacial and fluvio-glacial silts and sands and the lighter loams of the river terraces to the silty peat of the mixed cumulose and sedimentary deposits of the moss-margin and the purely cumulose deposits of the raw bog. Heavy land on the high ground and light land on the low ground is the general rule in this district.

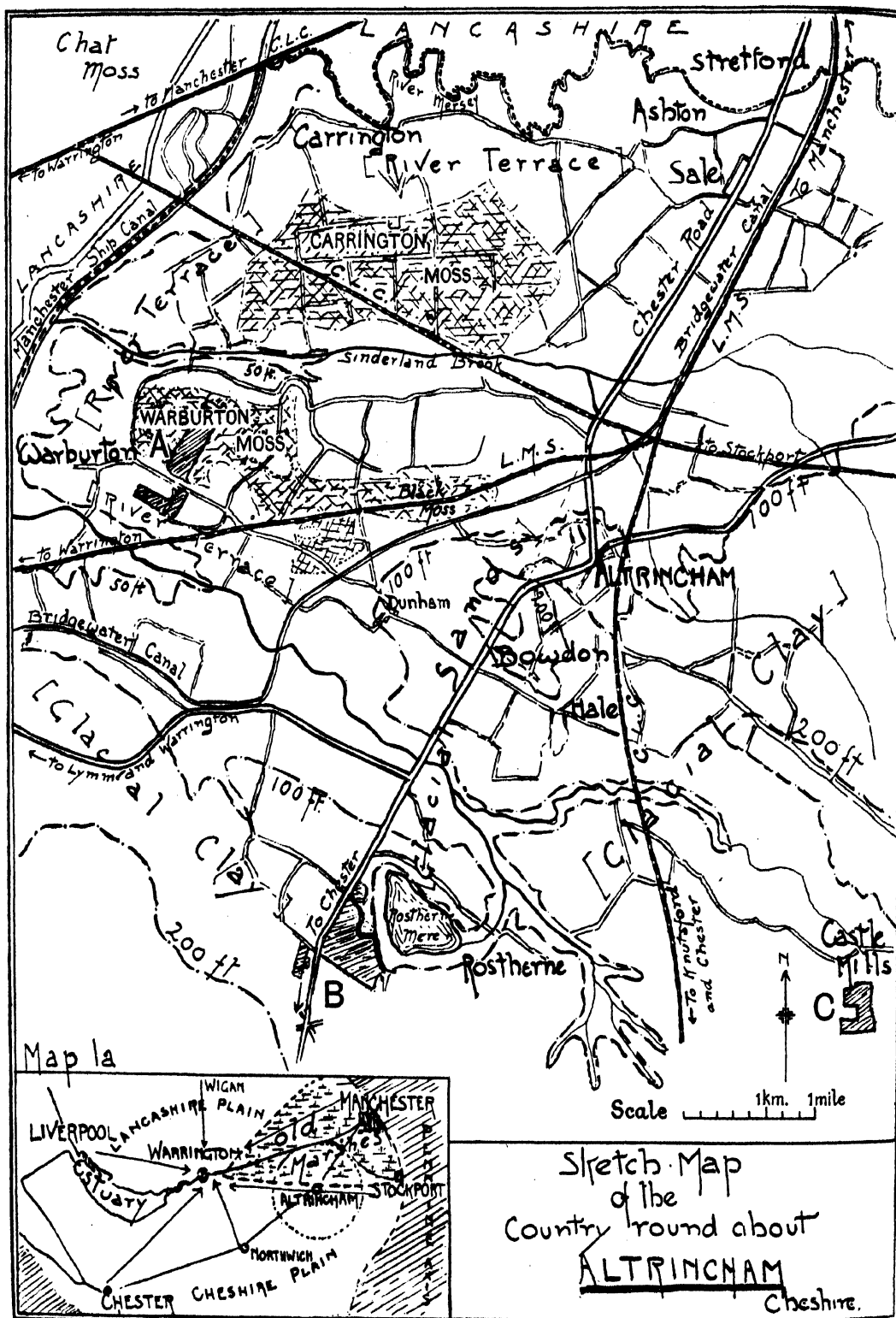
The division of the soils into broad classes, such as heavy, light, or peaty, is very convenient, and it may be said that the general conclusions drawn from the study of the association of plants with soil based on such a wide classification are tolerably correct; but great care needs to be exercised with respect to the sub-divisions: the soils pass imperceptibly into one another and it is often difficult and sometimes impossible to draw a line between them.

The nature of the sub-soil also is a matter of no small importance: deep soils, whether they be clayey, sandy, or peaty, though presenting problems of their own, are at least more or less clear in virtue of their uniformity; but shallow medium or light soils on stiff clay or shallow peaty soils on fine silt or clay are very confusing.

Settlements. The nature of the surface deposits is very largely reflected in the positions of the settlements and in the alignment of the main roads within the area: in early days choice of site was largely determined by the presence of potable water and of soil that would repay cultivation. In this district where there are deposits of sand, clay, and peat, the choice of site was largely restricted to the areas of sands: Altrincham, Bowdon, Hale, Dunham, Rostherne, and Knutsford are, for the most part, on glacial or fluvio-glacial sands or silts; Stretford, Sale, Ashton-on-Mersey, Carrington, Partington, and Warburton are on the "sands" of the river terraces.

The peaty deposits of the low ground to the north, at that time in the state of bog, were the least suitable of all as sites for human settlements; and in addition they presented an almost insuperable barrier to communication between settled areas.

The barrier of the Old Mersey Marshes. Topographically the mosslands belong to the area of the Old Mersey Marshes (Map 1a) which, with the river and its estuary, stood athwart the Western Plain between the Pennines and



Map 1.

the Irish Sea, barring the way to the north-west, except at two places—one at Warrington where certain local factors such as the tidal limit, the narrowing-down of the marshes, and the presence of firm ground in the bed of the river, determined the position of an ancient crossing-place (Latchford), and another on the firm ground between the marshes and the hills from Stockport to Manchester on “the immemorial marching road of the tribes¹.”

Lines of communication. The disposition of the main lines of communication within the area is thus determined by the presence of this barrier to the north and by the position of the ancient “key” towns of Manchester, Stockport, Warrington and Chester. It is also interesting to note that the course of the country roads in the mosslands reveals the same difficulty with respect to barriers: communication between village settlements and old farms² (which are situated almost without exception on the sands) was *round* the mosses and rarely across them. Thus the course of some of these roads is a rough guide to the boundary between the sands and the peats.

Some semi-natural plant communities. Carrington Moss and Warburton Moss (including Dunham Moss), the two largest mosses on the Cheshire side of the Mersey, are to-day almost entirely under cultivation: they are valuable additions to the arable lands within easy reach of large industrial towns. Warburton differs from Carrington in being less compact (more broken up by sandy ridges), and in having a smaller area of what originally was raw bog: much of its peaty deposits is shallow and highly decomposed, giving rise in parts to black soil known locally as “black moss.”

It has been stated previously that natural plant communities do not exist within the area: the most that can be said is that here and there are small patches of semi-natural vegetation (mostly woodlands) that have been allowed to remain because they serve some useful purpose such as acting as “cover,” or that have persisted, like the weeds of the farmland or the vegetation of the hedges and ditches, in spite of efforts to eradicate them.

Probably before cultivation the greater part of this district, but more especially the higher part, was covered with mixed woodland in which the pedunculate oak (the climatic climax) greatly predominated; in the low-lying part, where the soil was peaty and acid, were moss associations with birch-scrub or in the drier parts with birch-woods, of *Betula pubescens* (probably d.) and *B. verrucosa*—the edaphic climax; and in the wet but less acid parts of the low-land area and along the water-courses on the higher ground were swamp associations of alder, willow, and poplar.

¹ Hilaire Belloc, *Warfare in England*.

² Some of these farms are still supplied with drinking water from wells sunk in the sands: this water is often peaty and is boiled before use.

WARBURTON MOSS.

The sketch-map (Map 2) represents a transect across the moss from the Carrgreen Ridge to the silts and sands beyond Moss Wood, along the line of what is known locally as Moss Lane.

Despite great variation in the nature of the soil in the different parts of the area covered by this map, there is little difference in the crops raised, though there may be minor differences in the quality, quantity, or reliability of these crops, which are indications of the different conditions. For instance: the moss is pre-eminently a potato-land; but it is inferior to the surrounding lands as a corn-land: as arable land it is more difficult to work; for the soil is often distinctly acid and the drainage poor: the whole of the low-lying area is subject to frost and in point of time of harvesting it may be said to be about two weeks behind the rest of the district¹.

If the crops do not vary much, this cannot be said of the semi-natural vegetation. The latter indicates that in the natural state there were here three distinct belts: (1) communities on sandy, silty, gravelly and in parts clayey soil—mostly mixed woodlands in which the pedunculate oak predominated, (2) moss-marginal communities on silty peat in which such trees and shrubs as alder, willow, poplar, birch, mountain ash, oak, holly and alder buck-thorn predominated, and (3) communities on deep, acid peat.

A general survey of the floristic composition of some of these communities, in particular of those on the moss and on the moss-margin, may now be given.

(a) MOSS WOOD (MAP 2 a).

A. TREES: *Betula pubescens*² (dominant), *Pinus silvestris* (occasional), *Quercus robur* (and hybrids) (o.), *Pyrus aucuparia*, and *Alnus glutinosa* (scarce).

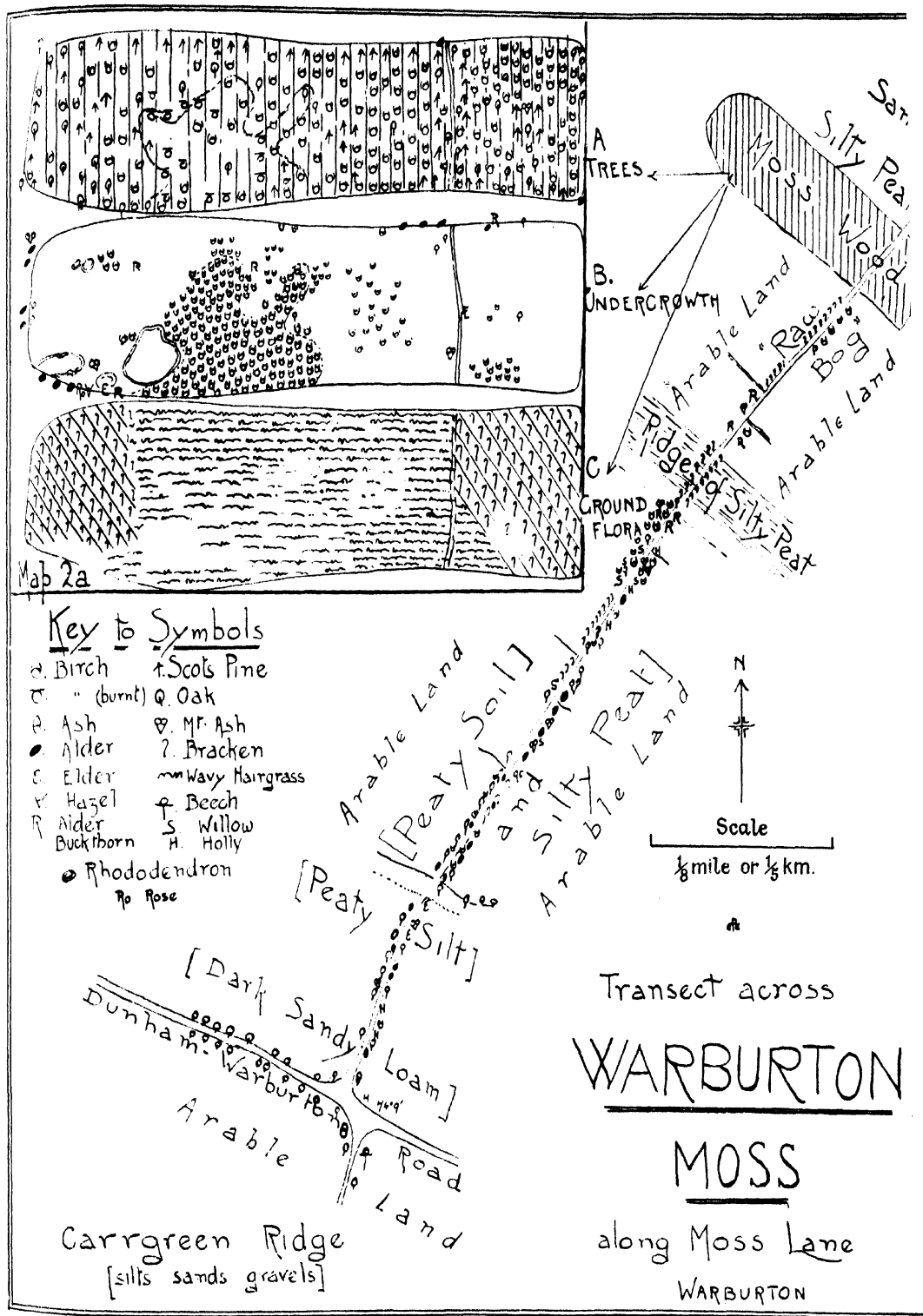
B. UNDERGROWTH: *Betula* (d. in parts), *Alnus glutinosa* (edges only), *Rhododendron* (in patches at one end: planted), *Rhamnus frangula* (o.), *Rubus* sp. (o. to frequent), *Pyrus aucuparia* (s.), *Rosa* sp. (s.), *Corylus avellana* (v.s.) *Ulex europæus* (v.s.), *Sambucus nigra* (v.s.).

C. GROUND-FLORA: (a) *Pteridium aquilinum* (fully d. at the two ends), (b) *Deschampsia flexuosa* (d.), *Dryopteris dilatata* (f.), *Galium saxatile* (f.), *Rumex acetosella* (dist. d. in patches under *Pinus*), *Digitalis purpurea* (f. to o.), *Epilobium angustifolium* (o. in clans), *Poa annua* and *Holcus lanatus* (o.).

Moss Wood (Phot. 1) is a plant community that has developed on a part of the moss during the last seventy years, i.e. since the time when the "raw bog" was first brought under cultivation: in that sense it is a natural community, though it is probable that some of the pine trees, at least, were planted. During this time many changes have taken place—the land has been drained,

¹ "In seasons the flora of the Peat is fully three weeks to a month behind that of gravelly or marly tracts at the same level" [*Flora of West Yorkshire*, by F. A. Lees, 1888].

² *B. pubescens* or some form of *pubescens* is the dominant tree here. Putative hybrids are also numerous; but no tree that could be definitely termed *B. verrucosa* was found.



Map 2.

some of the trees have been felled or burned and *Rhododendron* has been planted: on this account Moss Wood is in reality a semi-natural community in rank about midway between the purely natural and the purely artificial. The trees other than birch (mostly pine and oak) occur chiefly on the periphery and have little effect on the floristic composition of the community as a whole: the woodland thus, in effect, is a consociation of birch trees (*Betuletum*). Speaking generally, there is little undergrowth (Phot. 2) and most of the floor is occupied by bracken at the more open ends and by *Deschampsia flexuosa* in the remaining parts. Where bracken occurs there is little or no other form of vegetation, but with *Deschampsia flexuosa* are: societies of *Rumex acetosella*, *Galium saxatile* and *Dryopteris dilatata*, with clans of *Digitalis purpurea* and occasionally of *Epilobium angustifolium*. The oak trees are pedunculate forms and some of these are notable for the presence of small, often microscopic, stellate hairs on the under-side of the leaf. In this respect they resemble some of those on the moss-margin at Carrington and are probably hybrids between the pedunculate and the sessile forms, though much nearer the former^{1,2}.

During the great drought of the summer of 1921 a part of this woodland took fire: many of the trees were destroyed and the surface peat was reduced to wood-ash. To-day that part is characterised by a dense growth of young birches varying from five to nine feet in height. It may be of some interest to give the floristic composition of this "burn subseres" in 1922 and in 1927 respectively in a form showing relative abundance (Phot. 3).

| | 1922 | 1927 |
|---------------|---|--|
| DOMINANT: | <i>Betula</i> (seedlings) | <i>Betula</i> (shrubs) |
| SUB-DOMINANT: | | <i>Deschampsia flexuosa</i> |
| FREQUENT: | <i>Ceratodon purpureus</i> <i>Epilobium angustifolium</i> <i>Funaria hygrometrica</i> | <i>Dryopteris dilatata</i> |
| OCCASIONAL: | <i>Dryopteris dilatata</i> <i>Deschampsia flexuosa</i> <i>Galium saxatile</i> <i>Holcus lanatus</i> <i>Polytrichum</i> sp. <i>Rubus commune</i> <i>Rumex acetosella</i> | <i>Ceratodon purpureus</i> <i>Digitalis purpurea</i> <i>Epilobium angustifolium</i> <i>Funaria hygrometrica</i> <i>Polytrichum commune</i> <i>Pteridium aquilinum</i> <i>Rubus</i> sp. |
| SCARCE: | <i>Poa annua</i> | |

In 1922 all the plants except the birch seedlings occurred in clumps; but in 1927 *Deschampsia* had become the dominant species of the floor, covering the bare spaces and ousting the mosses, in particular.

Small fires occur sporadically, and in this way (through burning) the ground is prepared for the reception of new-comers; but unless this takes place seedlings of any kind of plant not already within the community fail to establish them-

¹ Evans, 1923.

² These forms are not entirely confined to the peats: a few of the oak trees on the Carrgreen Ridge of sands, silts, and gravels are of this nature (*Q. robur* × *sessiliflora*).



Phot. 1. A part of Moss Wood in the distance: oats on "raw-bog" in the fore-ground. In the centre of the wood is the "burn-subere," showing dead birch trees and a dense undergrowth of birch shrubs.



Phot. 2. A near view of a part of Moss Wood, showing the consociation (*Betuletum*) in its normal state, i.e. without undergrowth. The ground floor here is occupied mainly by the hair-grass (*Deschampsia flexuosa*). Note the "Birch Bracket" (*Polyporus betulinus*)—a very common fungus here—in the left fore-ground.



Phot. 3. A near view of a part of the "burn-subscere," showing the dead birch trees (still standing) and the dense undergrowth of birch shrubs (*Betula pubescens* and, probably, hybrids). In the fore-ground are *Deschampsia flexuosa* (dominant), *Dryopteris dilatata* (frequent) and *Epilobium angustifolium* (in flower and in fruit).



Phot. 4. A continuation of the view given in Phot. 1, showing the oat field on the left, a potato field on the right (both on "raw bog"), and "Moss lane" in the centre. The grasses shown are *Molinia* and *Deschampsia*, but the zonation, referred to in the text, is not clear because the grass in the centre of the lane had been mown before the photograph was taken. The open drains referred to are between the lane and the arable land.

selves, even where there are bare patches. Rabbits are present and their burrows occur where there is a fair proportion of sand with the peat or where the sands are near the surface, as in parts of Moss Wood and on the ridge of silty peat. The "kneed" appearance of the boles of many of the birch trees may be the result of attack by rabbits, though it is difficult to detect any evidence of their presence from markings on the bark of the seedlings¹.

It seems that by a process of burning in successive sections, thus leaving sufficient trees for the supply of seeds, the whole of this woodland could be regenerated in a comparatively short time.

(b) THE "RAW BOG."

Between Moss Wood and the ridge of silty peat is a thick deposit of brown peat resting on a bed of white (bleached) sand: this is a portion of true moss and the local name, "raw bog," is reminiscent of the time—within the memory of some of the oldest inhabitants—when this was a "wild" land of "bog and heather"—a spot of some local note for its whinberries (*Vaccinium myrtillus*). At the present day, heath (*Calluna vulgaris*) and whinberry have all but disappeared and practically the whole of the area has been brought under cultivation. Along the large open drains on each side of the lane, *Molinia coerulea*, *Deschampsia flexuosa* and a few stunted birches, in addition to some other plants less characteristic of mosslands, manage to maintain a foothold despite the repeated clearings to which these parts are subjected.

A study of the vegetation here is of interest not only because it shows how tenacious some of the relics of the natural flora can be, but also in showing how semi-natural plant communities resemble natural communities in their groupings (Phot. 4). Across Moss Lane from ditch to ditch—a distance of about ten yards—the vegetation shows a distinct zonation. The path in the centre, with patches of *Poa annua* and plants like *Nasturtium palustre*, *Stellaria media*, *Viola arvensis*, *Sagina procumbens*, and *Polygonum amphibium*—mostly invaders from the arable ground—is bounded on both sides by four grass zones, in order from the path as follows: the *Agrostis* zone, the *Holcus* zone, the *Deschampsia* zone, and the *Molinia* zone. These are followed by a lichen zone, on brown acid sphagnum peat exposed near the top of the drain, a liverwort zone on the lower sides of the drain near the water, and an algal zone in the drain.

In the grass zones are such plants as *Galium saxatile*, *Rumex acetosella*, *Potentilla procumbens*, *Digitalis purpurea*, *Betula verrucosa*, *Quercus robur* (*pedunculata*, a few stunted trees), and *Ulex europæus* (v.s.); the lichen zone is occupied almost entirely by *Cladonia floerkeana* Fr.; *Calypogeia trichomanis* dominates the liverwort zone; and in addition to such plants as *Juncus communis*, *Poa fluitans*, and *Dryopteris dilatata* mostly on the sides of the

¹ Farrow, 1915-1924.

drain, a rather specialised group of plants inhabits the water in the drain—a group comparatively poor alike in the number of genera and species but in some cases rich in the number of individuals of the same species.

The periodic clearing of the drain, the drying-up of the water in summer and above all the extremely acid condition at certain seasons, are the factors that determine both the composition and the relative abundance of the flora here.

There is present in the drain a fair number of diatoms of which *Navicula* is the dominant genus and *viridis* a frequent species; a characteristic peat-loving plant—*Microthamnion Kützingianum* Näg.; some quantity of *Mougeotia* (? *M. parvula* Haas) and of a species of *Gonatozygon* with a perfectly smooth cell-wall—*G. Kinahani* (Arch.) Rabenh. forma; a species of *Microspora*—probably *M. stagnorum* (Kütz) Lagerheim, and of *Tribonema*; and *Volvox globator* (scarce). In the shallow end of one of the ditches there is a fair quantity of *Sphagnum cymbifolium* Ehrh. and *Fontinalis antipyretica* L.

In one part of this section and along the ditches are clans of *Epilobium angustifolium*, forming centres from which the burnt patches in Moss Wood are colonised.

From a study of the relics of the old vegetation and from a consideration of some historical facts it may be permissible to infer that by about the middle of last century the moss associations of the “raw bog” had largely given way to heath associations preparatory to the passing of the land, with further desiccation, into a birch-scrub or a birch-wood—the edaphic climax. [Sphagnetum → Callunetum → Betuletum.]

(c) MOSS-MARGINAL VEGETATION.

The “raw bog” is bounded on its southern side by a ridge of silty peat—“hungry” soil, which on arable land produces inferior crops and on the lane which crosses it bears a dense growth of bracken. Between this ridge and the edge of the moss near the Warburton-Dunham road is a region where the soil is of black peat in parts and of brown silty peat in others, overlying sandy, silty, or even clayey deposits which are near enough to the surface to have an important effect on the vegetation. Such areas near the margin of peat-mosses, where the drainage is defective, the peaty soil thin and acid (but less acid than the true moss), are characterised by vegetation distinct from that on the brown, thick, acid peat of the true moss: such vegetation may be designated “moss-marginal.” Characteristic plants here are: *Alnus*, *Salix*, *Betula*, *Pyrus aucuparia*, *Ilex*, *Quercus robur* (and many putative hybrids with minute stellate hairs on the leaves), *Rhamnus frangula*, *Agrostis vulgaris*, *Digitalis purpurea*, *Galium saxatile* and *G. palustre*, *Deschampsia flexuosa* (but not usually *Molinia caerulea*). Amongst others here also are: *Dryopteris dilatata*, *Athyrium filix-faemina* and, in the drain, *Callitriche aquatica*, *Lemna minor* and *Zygnema cruciatum*.

WEEDS OF ARABLE LAND.

Weeds of arable land are a semi-natural plant community or a group of such communities not very far removed from the purely artificial group—the crops of the farmland—amongst which they grow. In the spontaneity of their growth they are natural: according to habitat they are artificial. On account of this dual nature special attention must be given to the operation of factors resulting from some definite form of human activity, as well as to the action and interaction of the factors governing the growth of plants in a state of nature. The often indeterminate and always variable nature of the human biotic factors renders the study of weeds difficult, and often precludes the drawing of any but very general conclusions.

This survey embraces the study of weeds of arable ground on all the main types of soil except chalk, amongst all the chief crops except barley, and during a period—four years—when most of the fields under observation passed through a complete rotation.

Rotation of crops. The crops¹ grown on the farms included in this survey may be taken as typical of those grown on the farmlands in the district in general, omitting those of “market-garden” type which are raised in large quantities on the low-lying grounds within easy reach of large towns. The system of rotation commonly practised, or at least aimed at, is a four-course shift as follows: roots², wheat, oats, clover³, with variations in the order of the crops on some of the farms and even on the same farm, according to considerations of weather, market, soil, labour, and the state of the ground with respect to weeds, insect pests and so on.

Thus at Carrington on the moss (Moss Hall: an arable farm) the normal shift is followed; but at Brookheys (a mixed arable and dairy farm) on the margin clover is repeated for a second year so that normally two-fifths of the land is under this crop: at Warburton on the “raw bog” a three-course shift is adopted—roots, corn (usually oats), clover; but on the moss-margin the usual rotation is—roots, wheat, clover, oats, with oats sometimes preceding clover as in the normal shift: at Carr Green (arable farm) on the ridge of good, light to medium loamy soil the usual order is—roots, oats, clover, wheat; but sometimes, when the ground is overrun with “dother” (*Spergula* spp. locally “Carrgreen clover”) and when there is a strong clover root, clover is repeated for the second year: at Rostherne (Denfield Hall⁴: mixed arable and dairy

¹ It is interesting to note that sugar-beet was grown on one of these farms for two seasons in succession; but after a fair trial it cannot be said that the experiment was a financial success.

² The term roots is used for such crops as potatoes, mangolds and so on.

³ Clover here includes grasses.

⁴ At Denfield Hall the system of rotation has been changed and the shift—roots, wheat, oats clover—has been adopted with better results, at least as far as the oat-crop is concerned. Despite most efficient farming it was found that the oat-crop following clover was often a comparative failure owing to the ravages of the grub of the crane fly. This larva feeds chiefly on the roots of

farm) on very good, mostly medium land, the rotation aimed at is—roots, wheat, oats, clover (repeated for another year if the root is good), oats; but at Castle Mills¹ (Castle Hill: dairy farm) on heavy or very heavy land two or three clover leys in succession are included in the rotation.

At Rostherne the best crops are oats, potatoes and wheat and at Carr Green potatoes, oats, clover, wheat, in the order named. On the moss at Warburton and on the moss-margin potato is the best and the most successful crop unless it is caught by late frosts. Oats come next in importance, though the yield is often inferior to that on other soils in the district: the grain may be described as light or “poorly fed.” On the actual “raw bog” winter wheat rarely forms part of the rotation; but spring wheat is sometimes grown with fairly successful results. There is always here, on acid peaty soil, a difficulty in establishing a clover root, and the clover crop, with the exception of white clover which does best on this sour land, is rarely satisfactory; but clover is included in the rotation because it plays an important part in the amelioration of the soil. Again, on this low-lying peaty land the success of the crops is more than usually dependent on the season: a medium season is the best; but a dry season is better than a wet one.

The inclusion of roots, at least once every four years, ensures a thorough cleansing of the land—an essential process on some of the light or medium land overrun with spurry or on wet low-lying weed-infested parts of the moss-margin. In most cases potatoes follow clover in the rotation: potatoes seem to thrive best after a clover crop and in an area within easy reach of large industrial towns potato is a most valuable crop.

Manure. Farmyard manure is supplemented in some cases with “town” manure (horse, stable manure) and in most cases with artificial manure such as sulphate of potash, superphosphate, and sulphate of ammonia: sometimes mustard and rape are grown to be ploughed in as green manure. On the “raw bog” at Warburton, after the original “wild” surface had been cleared and the land drained by horse-shoe pipes opening out into large open drains, “night-soil,” at the rate of 25 tons per statute acre, was dumped on the surface. This was wheeled to the fields in barrows run on planks to prevent sinking;

grasses, and when the grass was ploughed in and oats sown the larvae played havoc with the roots of the oat plants.

On some farms the use of Paris Green has been attended with some success, but the biggest factors of successful control are: good cultivation, including the rolling of the ground in the early morning before sunrise when the grubs are on the surface; the application of forcing manures, such as sulphate of ammonia and nitrate of soda, which help the crops in the early stages, after which the grub has little or no effect (Wilkins, 1927, pp. 192–194); and, as in the above case, the adoption of a system of rotation that gives the grub little or no encouragement.

The sowing of spring oats as early as is practicable in soil of good tilth, and (if necessary) top dressing, give the crop a good start and strengthen it against possible attack by another pest the Frit Fly (*Oscinis frit*).

¹ This farm has changed hands lately: it is now a stock farm almost entirely under grass.

and even to this day this land is not workable at certain seasons, because horses cannot be employed as they tend to sink into the peat.

Lime. The application of lime is fairly general, followed it is believed by very good results. A notable exception, however, is the "made" soil on Moss Hall farm, Carrington, where lime has no appreciable effect except perhaps a deleterious one¹. Lime is applied regularly on Warburton Moss (Mr Pennington), at Carr Green (Mr Beckett), and at Rostherne (Mr Pimlott): at Carr Green 30 cwts. per acre are put into the ground once during a complete rotation, usually after roots; at Denfield Hall it is applied before clover. Where the ground is naturally acid, and where sulphate of ammonia and superphosphate are applied, lime is essential to the production of good crops: the addition of lime increases the solubility of the phosphate² and counteracts the acidifying effect of the ammonia fertiliser.

Soil reaction. Failing a detailed and systematic soil survey the following notes, which are based on simple experiments on soil reaction, may be of some value. Samples of soil were taken from certain parts of the area and then air-dried; from each sample one gram was taken and thoroughly mixed in a test-tube with 10 c.c. of distilled water, and after the bulk of the suspended matter had settled a small volume of the more or less clear liquid was mixed with an equal volume of a suitable indicator. The resulting colour was then compared with a chart of "buffer" solutions, called a capillator, showing the gradation of colour change of the same dye solution (indicator) according to the degree of acidity or alkalinity as the case may be.

It may be stated, provisionally³, that the glacial clays are neutral or only slightly acid, the glacial sands and silts slightly to moderately acid, the silty peats acid, and the brown peat of the raw bog very acid.

¹ This may be due to the effect of the "night-soil," hundreds of thousands of tons of which were dumped on the moss.

² Wilkins, 1927, p. 25.

³ The following is a list of some pH determinations:

| | | |
|--|--|-----|
| (a) Peaty soil: | uncultivated surface, Moss Wood, Warburton | 4.4 |
| | 2 feet below the surface, Moss Wood, Warburton | 4.0 |
| | 3 feet below the surface, Moss Wood, Warburton | 3.8 |
| | cultivated surface, "raw bog" near Moss Wood | 6.3 |
| | 2 feet below the surface, moss-margin | 4.7 |
| (b) Post-glacial sands: (river terrace) | cultivated surface, moss-margin | 6.2 |
| | cultivated surface, "Black Moss" (Dunham) | 6.6 |
| | uncultivated surface (Carr Green) | 6.0 |
| | 3 feet below the surface (Carr Green) | 5.7 |
| | cultivated surface (Carr Green) | 6.6 |
| (c) Glacial sands and silts: | uncultivated surface (Castle Hill) | 6.5 |
| | 3 feet below surface (Castle Hill) | 6.7 |
| | 9 feet below surface (Rostherne) | 6.1 |
| | cultivated surface (Rostherne) | 6.4 |
| | cultivated surface (Castle Hill) | 6.9 |
| (d) Glacial clay: (Boulder clay) | uncultivated surface (Castle Hill) | 6.7 |
| | 3 feet below surface (Rostherne) | 6.4 |
| | cultivated surface (Rostherne) | 6.5 |
| | cultivated surface (Castle Hill) | 7.1 |

[Soils below pH 5 are distinctly acid (sour), between pH 5 and pH 7 moderately to slightly acid soils about pH 7 are neutral; soils with a pH value above 7 are alkaline.]

Drainage. Speaking generally, the drainage of the district may be said to be efficient on the sloping intermediate ground, but hardly so on some of the flat lands on the higher ground to the south or on the low-lying ground to the north. At Castle Mills (Castle Hill farm) on very heavy ground the drains are much too deep—2 ft. 6 in. to 3 ft., and sometimes more, from the surface—and a study of the weeds (*Alopecurus geniculatus* for instance) shows that the ground is often sodden: at Warburton on the moss there is not sufficient gradient to ensure good drainage, and on the “raw bog,” owing to shrinkage (the arable land is below the level of Moss Lane), the old horse-shoe pipes, and incidentally some large tree-roots, have worked to the surface and the land has had to be re-drained.

The use of marl in old days. Much of the land in this district has been marled at one time or another. Attempts were made to improve certain parts of the moss-margin at Warburton in this way: at Rostherne (Denfield Hall) marl was dug and carted on to the fields during what were termed “boon days¹.”

In the introduction to Lord de Tabley's *Flora of Cheshire* the following passage occurs with reference to the marl pits. “Now as to the pits. The word possesses a distinct provincial connotation, meaning an excavation of the surface for marl, which, when disused, rapidly fills with water. The pits, usually in fields², not at road sides like ponds, are seldom either large or deep, say from 15 to 60 yards in diameter and often circular. In old days, before the introduction of foreign or artificial manures, the efficacy of marl was greatly believed in as a renovator of the soil; and as in Bucklow one has generally only to dig for it to procure it, nearly every old Cheshire field has its appropriate marl pit which remains sufficiently obvious to the present day. When three or four small fields have been thrown into one by improved farming, the united field remains with as many pits within its single circuit. When marl was scarce and holdings were small, two or more pits were excavated side by side, or rather back to back by separate occupiers, or at different dates, the old pit having become water-logged. The narrow ridge of surface land between two marl pits is locally called a ‘mid-feather².’”

Weeds and soil. Of 310 records, 99 were on fields of silty peat, 92 on fields of light loamy soil, 51 on medium, 51 on heavy soil, and 17 on “raw bog.”

The *percentage* figures in the tables (below) are therefore most reliable with respect to silty peat and light soil, and least so with respect to the “raw bog.”

Weeds and crops. The records concerning peas and beans (8 in all) are

¹ Boon work was service paid in labour on the lord's demesne at times during the year when such work was required. Boon days, in this case, were times when neighbouring farmers helped one another on the land: this is not strictly boon work, but the use of the term almost within living memory is of interest as a survival from the time when such work was compulsory.

² Not all pits in fields are marl pits: some were dug for clay to make bricks for building the farmhouse (Denfield Hall farm).

omitted owing to their scantiness and this leaves a total of 302, of which 113 are for oats, 100 for roots, 50 for clover, and 39 for wheat.

The *percentage* figures in this case are most reliable for oats and roots and least reliable for wheat and clover. Wheat did not form part of the rotation on "raw bog" or on the very heavy ground at Castle Hill during the time that the fields were under observation.

The tables that follow include all the weeds that were seen on the arable land covered by this survey.

The figures at the top of the columns refer to the number of records taken for each heading. Since many of the fields were under observation for four years the figures do not imply that number of separate fields or units.

"Percentage frequency" is the number of times seen per hundred fields or units examined.

"Raw bog" is a term used throughout this paper for arable ground on thick acid peat: about 70 years ago this land was raw bog in actuality.

"Silty peat" denotes a thin layer of black peat, or of peat with silt, on a layer of sand, silt, or clay.

In the last column the remarks refer to this survey alone: they are conclusions drawn very largely from the figures in the tables.

This list consists of 33 weeds of which 17 are annuals and 16 are perennials. All are "natives" of the county except *Papaver dubium*, which may be described as a "colonist," and all are "generally distributed" in the same area except the above-named and *Galeopsis versicolor* which may be described as "local."

Some, like *Nasturtium palustre* and *Polygonum amphibium*, are practically confined to one type of soil, but may be pests on that soil; some, like *Capsella bursa-pastoris* and *Senecio vulgaris*, occur on all soils but cannot be said to have any great deleterious effect on the crops; and others, like *Polygonum persicaria*, *Rumex acetosella* and *Spergula* spp., occur in such quantities that they rank as the most pernicious of all weeds and their eradication or suppression is of the utmost importance. Fifteen weeds of this last class, which may be termed the worst weeds on the ground surveyed, are given in the tables below (III and IV) with notes and figures concerning their relative abundance in association with soils and crops.

Alopecurus geniculatus, the kneed water-grass, may be said to be characteristic of heavy land on which water stagnates during winter: when these conditions prevail and when the plant is present at all, its method of spreading and rooting at the nodes enables it to establish itself and to become fully dominant.

Poa trivialis also shows a preference for heavy land and tends to become dominant on such soil in the second or third year leys; but as it is often introduced with the seed mixture it is difficult to determine its natural distribution.

Juncus bufonius occurs chiefly on damp soil or on soil with an impervious

Table I. Weeds and soil (dominant and sub-dominant species).

| Name | Times seen | Percentage frequency | | | | | Times dom. or sub- dom. | Remarks |
|---|---------------|----------------------|-------|--------|-------|---------------|-------------------------------------|---|
| | | All soils | Heavy | Medium | Light | Silty peat | Raw bog | |
| Agrostis spp. (Bent grass) | 194 | 63 | 73 | 53 | 60 | 73 | 6 | All soils: much less on "raw bog" |
| Alopecurus geniculatus (Marsh foxtail) | 25 | 8 | 27 | 17 | 2 | 0 | 0 | Characteristic of wet, heavy land: absent on peaty soil |
| Anagallis arvensis (Scarlet pimpernel) | 43 | 14 | 43 | 27 | 6 | 1 | 0 | Preference for heavy or medium heavy land: scarce on peaty soil |
| Atriplex patula (Orache) | 103 | 33 | 69 | 35 | 12 | 34 | 29 | All soils: preference for heavy land |
| Brassica campestris (Field brassica) | 37 | 12 | 2 | 6 | 13 | 21 | 0 | Preference for light soil and silty peat |
| Capsella bursa-pastoris (Shepherd's purse) | 33 | 11 | 8 | 8 | 17 | 7 | 12 | All soils |
| Chenopodium album (Fat hen) | 78 | 25 | 31 | 10 | 16 | 35 | 41 | All soils |
| Cirsium arvense (Creeping thistle) | 102 | 33 | 65 | 27 | 32 | 25 | 0 | More on heavy land: absent from "raw bog" |
| Equisetum arvense (Horse-tail) | 199 | 64 | 71 | 90 | 67 | 56 | 0 | All soils except "raw bog": more on medium or heavy soil |
| Galeopsis spp. (Hemp nettle) | 127 | 41 | 2 | 35 | 37 | 65 | 65 | Preference for peaty soil: scarce on heavy land |
| Gnaphalium uliginosum (Marsh cudweed) | 79 | 25 | 4 | 31 | 31 | 26 | 35 | All soils: much less on heavy land |
| Holcus lanatus (Yorkshire fog) | 94 | 30 | 59 | 33 | 16 | 27 | 29 | All soils: more on heavy land |
| Juncus bufonius (Toad rush) | 44 | 14 | 6 | 29 | 9 | 15 | 12 | All soils: more on medium soils on heavy sub-soil |
| Mentha arvensis (Corn or field mint) | 113 | 36 | 0 | 10 | 22 | 80 | 53 | Characteristic of wet peaty land |
| Myosotis versicolor (Corn scorpion grass) | 82 | 26 | 35 | 4 | 12 | 36 | 88 | Preference for peaty land |

| | | | | | | | | | |
|---|-----|----|----|----|----|----|----|-----|--|
| Nasturtium palustre (Marsh watercress) | 13 | 4 | 0 | 0 | 0 | 3 | 18 | 4 | Characteristic of "raw bog" |
| Papaver dubium (Long headed poppy) | 17 | 5 | 0 | 0 | 12 | 5 | 6 | 1 | Characteristic of light soil |
| Plantago lanceolata (Ribwort plantain) | 20 | 6 | 16 | 6 | 2 | 6 | 6 | 1 | All soils |
| Plantago major (Greater plantain) | 69 | 22 | 67 | 39 | 7 | 5 | 18 | 2 | Preference for heavy land |
| Poa annua (Annual meadow-grass) | 166 | 54 | 76 | 76 | 39 | 42 | 59 | 25 | All soils: more on heavy or medium land |
| Poa trivialis (Rough-stalked meadow-grass) | 42 | 14 | 55 | 10 | 5 | 4 | 0 | 8 | Characteristic of heavy land |
| Polygonum amphibium (Amphibious polygonum) | 53 | 17 | 0 | 4 | 0 | 43 | 47 | 4 | Characteristic of peaty land |
| Polygonum aviculare (Knot-grass) | 157 | 51 | 65 | 71 | 34 | 43 | 18 | 9 | All soils: more on medium or heavy land |
| Polygonum persicaria (Willow-weed) | 238 | 77 | 69 | 78 | 70 | 87 | 76 | 118 | All soils: especially abundant on wet land |
| Ranunculus acris (Crowfoot) | 17 | 5 | 25 | 2 | 2 | 1 | 0 | 1 | Characteristic of heavy land |
| Ranunculus repens (Creeping buttercup) | 154 | 50 | 96 | 69 | 37 | 36 | 0 | 12 | Preference for heavy soil, absent from "raw bog" |
| Rumex acetosella (Sheep's sorrel) | 237 | 76 | 20 | 90 | 95 | 82 | 94 | 92 | All soils: very much less on heavy land |
| Senecio vulgaris (Groundsell) | 93 | 30 | 27 | 22 | 38 | 31 | 12 | 2 | All soils |
| Sinapis arvensis (Charlock) | 53 | 17 | 25 | 8 | 14 | 23 | 12 | 4 | All soils |
| Spergula spp. (Corn spurry) | 243 | 78 | 47 | 82 | 89 | 84 | 76 | 128 | All soils: much less on heavy land (scarce on very heavy land) |
| Stellaria media (Chickweed) | 193 | 62 | 73 | 63 | 60 | 61 | 53 | 39 | All soils: most on heavy land |
| Trifolium minus (Lesser clover) | 18 | 6 | 25 | 6 | 2 | 0 | 0 | 1 | Preference for heavy soil: absent from "raw bog" |
| Viola spp. (arvensis group) (Wild pansy) | 128 | 41 | 6 | 10 | 45 | 71 | 82 | 14 | Characteristic of peaty land |

* Number of separate records for the five columns: 310.

sub-soil: it is often present in such quantities on this type of soil that it blunts the edge of the cutting machine.

Nasturtium palustre, as a weed of arable land, is here confined to "raw bog": it is frequently dominant over small areas, notably in slight hollows, but in one case after the clover crop had been mown it covered the whole surface of the field like matting.

Polygonum amphibium (variety *terrestre*; locally called "wild within"), which, like *Nasturtium palustre* and *Rumex acetosella*, is a most pernicious weed on raw bog, occurs in greater quantities on arable land at Warburton than at Carrington, where it is confined to the edges. Like *Nasturtium palustre* it is "local" in its distribution even on the moss.

Papaver dubium was the only species of poppy met with on the land surveyed: though it was once found dominant in a small area, its distribution may be described as "occasional" in general but sometimes "frequent." At one time it could be said that "a poppy of any kind is in Bucklow a rarity¹" (*Flora of Cheshire*).

The system of rotation may be regarded as a kind of artificial succession in which crops of corn and roots, which leave a large proportion of the surface of the ground uncovered, are early stages of a "crop-subseres," and the clover crops, which normally cover the whole surface, are later stages: ordinary farmland weeds flourish in the early but are suppressed in the later stages. Advantage is taken of this peculiarity of the clover crops as an aid in the suppression of weeds; but though suppressed the weed-pest may not be eradicated. For example: in a field at Rostherne which was ploughed and set with oats after having been pastured for two years, spurry was abundant; and again, in another field set down in pasture about five years ago on account of the prevalence of this weed, small black seeds of spurry are plentiful in the sod and some are still capable of germination.

When the system of rotation includes two or three years ley the crop tends to deteriorate: the perennial weed-flora gradually gains the upper hand and tends to smother the crop. On this account this form of rotation is not suited to the weedy lands on the moss-margin and even on heavy ground (as at Castle Mills) in the third year the land becomes infested with such weeds as *Ranunculus repens* and *Alopecurus geniculatus*.

If "cultivation" did not take place it is difficult to tell how weeds would behave with root-crops; but after the cleaning process has been accomplished the figures show that next to clover the root-crops are associated with the smallest amount of weeds. In some cases, as for instance the weed-infested fields on the borders of the mosses, roots are grown for two years in succession.

¹ This certainly is not true to-day and therefore there must be an increase of poppy in this district since 1899 when the *Flora* was published. Dr **Brenchley** writes: "The increase of poppy in your district is noteworthy—we have the same thing on Broadbalk wheat field here [Rothamsted in Hertfordshire], on heavy land."

Table II. *Weeds and crops (dominant and sub-dominant species).*

| Name | Times seen | Percentage frequency | | | | Remarks |
|------------------------------------|---------------|----------------------|-------|------|-------|---------|
| | | All crops | Wheat | Oats | Roots | |
| | | | 39 | 113 | 100 | 50* |
| <i>Agrostis</i> spp. | 191 | 63 | 54 | 64 | 68 | 60 |
| <i>Alopecurus geniculatus</i> | 25 | 8 | 10 | 5 | 1 | 28 |
| <i>Anagallis arvensis</i> | 43 | 14 | 5 | 15 | 23 | 4 |
| <i>Atriplex patula</i> | 101 | 33 | 41 | 36 | 43 | 2 |
| <i>Brassica campestris</i> | 37 | 12 | 8 | 15 | 13 | 0 |
| <i>Capella bursa-pastoris</i> | 33 | 11 | 26 | 6 | 11 | 0 |
| <i>Chenopodium album</i> | 76 | 25 | 38 | 38 | 17 | 2 |
| <i>Cirsium arvense</i> | 102 | 34 | 36 | 34 | 36 | 28 |
| <i>Equisetum arvense</i> | 197 | 65 | 85 | 58 | 74 | 50 |
| <i>Galeopsis</i> spp. | 127 | 42 | 72 | 27 | 32 | 2 |
| <i>Gnaphalium uliginosum</i> | 75 | 25 | 28 | 27 | 31 | 4 |
| <i>Holcus lanatus</i> | 93 | 31 | 28 | 25 | 16 | 88 |
| <i>Juncus bufonius</i> | 44 | 15 | 36 | 11 | 4 | 26 |
| <i>Mentha arvensis</i> | 111 | 37 | 41 | 45 | 34 | 20 |
| <i>Myosotis versicolor</i> | 82 | 27 | 38 | 37 | 7 | 36 |
| <i>Nasturtium palustre</i> | 13 | 4 | — | 7 | 3 | 4 |
| <i>Papaver dubium</i> | 16 | 5 | 26 | 3 | 4 | 0 |
| <i>Plantago lanceolata</i> | 20 | 7 | 3 | 2 | 4 | 26 |
| <i>Plantago major</i> | 69 | 23 | 15 | 18 | 26 | 32 |
| <i>Poa annua</i> | 163 | 54 | 92 | 47 | 36 | 76 |
| <i>Poa trivialis</i> | 42 | 14 | 18 | 14 | 2 | 34 |
| <i>Polygonum amphibium</i> | 53 | 17 | 13 | 25 | 13 | 14 |
| <i>Polygonum aviculare</i> | 155 | 51 | 87 | 55 | 59 | 2 |
| <i>Polygonum persicaria</i> | 231 | 76 | 90 | 93 | 91 | 0 |
| <i>Ranunculus acris</i> | 17 | 6 | 0 | 2 | 0 | 30 |
| <i>Ranunculus repens</i> | 154 | 51 | 56 | 38 | 48 | 82 |
| <i>Rumex acetosella</i> | 233 | 77 | 97 | 80 | 71 | 66 |
| <i>Senecio vulgaris</i> | 88 | 29 | 44 | 28 | 36 | 6 |
| <i>Sinapis arvensis</i> | 51 | 17 | 26 | 22 | 14 | 2 |
| <i>Spergula</i> spp. | 237 | 78 | 100 | 91 | 88 | 14 |
| <i>Stellaria media</i> | 189 | 63 | 82 | 75 | 67 | 10 |
| <i>Trifolium minus</i> | 21 | 7 | 0 | 1 | 4 | 26 |
| <i>Viola</i> spp. (arvensis group) | 128 | 42 | 51 | 51 | 33 | 34 |

* Maximum for the four columns: 302.

Table III. *The fifteen worst weeds in relation to soil.*

| | Raw bog (17) | | | | | Silty peat (99) | | | | | Light loam (92) | | | | | Heavy loam (51) | | | | | Medium loam (51) | | | | | | | | | | |
|------------------------------|--------------|---|---|----|---|-----------------|----|----|----|----|-----------------|-----------|----|----|----|-----------------|---|-----------|----|----|------------------|----|---|-----------|----|----|----|----|----|-----------|----|
| | D | s | f | o | r | % abd. | D | s | f | o | r | % abd. | D | s | f | o | r | % abd. | D | s | f | o | r | % abd. | D | s | f | o | r | % abd. | |
| <i>Agrostis</i> spp. | 0 | 0 | 0 | 1 | 0 | 2 | 2 | 3 | 24 | 43 | 0 | 36 | 2 | 2 | 21 | 31 | 1 | 32 | 2 | 1 | 11 | 23 | 0 | 36 | 1 | 0 | 10 | 16 | 0 | 26 | |
| <i>Atriplex patula</i> | 0 | 1 | 0 | 4 | 0 | 14 | 0 | 2 | 11 | 20 | 1 | 17 | 0 | 0 | 0 | 8 | 3 | 4 | 7 | 10 | 7 | 10 | 1 | 46 | 4 | 0 | 4 | 6 | 4 | 19 | |
| <i>Cirsium arvense</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 22 | 3 | 9 | 2 | 0 | 5 | 21 | 2 | 15 | 1 | 0 | 5 | 23 | 4 | 27 | 0 | 0 | 5 | 7 | 2 | 12 | |
| <i>Equisetum arvense</i> | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 13 | 36 | 0 | 28 | 13 | 3 | 8 | 37 | 1 | 38 | 6 | 1 | 10 | 19 | 0 | 40 | 2 | 1 | 16 | 25 | 2 | 45 | |
| <i>Galeopsis</i> spp. | 1 | 0 | 2 | 8 | 0 | 32 | 1 | 4 | 24 | 35 | 0 | 33 | 0 | 0 | 2 | 24 | 8 | 13 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 17 | 0 | 13 |
| <i>Mentha arvensis</i> | 0 | 1 | 2 | 6 | 0 | 26 | 1 | 2 | 43 | 33 | 0 | 42 | 0 | 0 | 5 | 14 | 1 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 4 | 0 | 4 |
| <i>Poa annua</i> | 0 | 0 | 4 | 6 | 0 | 28 | 2 | 0 | 9 | 31 | 0 | 20 | 2 | 5 | 14 | 15 | 0 | 22 | 2 | 1 | 18 | 18 | 0 | 41 | 10 | 3 | 11 | 15 | 0 | 49 | |
| <i>Polygonum aviculare</i> | 0 | 0 | 0 | 3 | 0 | 7 | 0 | 0 | 3 | 40 | 1 | 18 | 0 | 0 | 0 | 41 | 0 | 18 | 4 | 5 | 7 | 17 | 0 | 37 | 0 | 0 | 4 | 32 | 0 | 30 | |
| <i>Polygonum convolvulus</i> | 0 | 0 | 0 | 5 | 0 | 12 | 0 | 0 | 12 | 48 | 3 | 27 | 0 | 0 | 3 | 40 | 4 | 20 | 0 | 0 | 2 | 13 | 3 | 14 | 0 | 0 | 2 | 18 | 0 | 16 | |
| <i>Polygonum persicaria</i> | 5 | 5 | 2 | 1 | 0 | 62 | 35 | 26 | 18 | 7 | 0 | 70 | 4 | 8 | 20 | 32 | 0 | 38 | 7 | 3 | 14 | 11 | 0 | 44 | 12 | 13 | 12 | 3 | 0 | 60 | |
| <i>Ranunculus repens</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 5 | 30 | 0 | 16 | 0 | 0 | 2 | 30 | 2 | 15 | 8 | 3 | 22 | 16 | 0 | 59 | 0 | 0 | 6 | 28 | 1 | 29 | |
| <i>Rumex acetosella</i> | 3 | 3 | 4 | 6 | 0 | 60 | 15 | 17 | 23 | 26 | 0 | 53 | 16 | 36 | 20 | 15 | 0 | 68 | 0 | 0 | 0 | 5 | 2 | 5 | 1 | 1 | 15 | 29 | 0 | 44 | |
| <i>Spergula</i> spp. | 0 | 1 | 1 | 10 | 1 | 33 | 25 | 9 | 26 | 22 | 1 | 57 | 57 | 11 | 8 | 4 | 1 | 79 | 0 | 0 | 3 | 18 | 3 | 19 | 18 | 7 | 9 | 8 | 0 | 63 | |
| <i>Stellaria media</i> | 0 | 0 | 2 | 7 | 0 | 24 | 5 | 11 | 26 | 17 | 1 | 37 | 1 | 2 | 10 | 42 | 0 | 28 | 12 | 3 | 12 | 9 | 1 | 50 | 4 | 1 | 6 | 21 | 0 | 33 | |
| <i>Viola</i> spp. | 2 | 3 | 5 | 4 | 0 | 53 | 6 | 3 | 25 | 35 | 1 | 38 | 0 | 0 | 17 | 21 | 0 | 20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 4 | 3 | |

In this table: D = dominant, s = sub-dominant, f = frequent, o = occasional, r = rare, % abd. = percentage abundance.

The number in brackets after the soil signifies the number of fields or units examined: thus silty peat (99) = 99 fields of silty peat surveyed.

The percentage abundance is calculated by using a scale, thus: dominant = 5, sub-dominant = 4, frequent = 3, occasional = 2, rare = 1. In order to obtain the maximum points on the scale the number of fields is multiplied by 5.

For example: *Atriplex patula* on heavy loam

$D = 7 \times 5 = 35$ points, $s = 10 \times 4 = 40$ points, $f = 7 \times 3 = 21$ points, $o = 10 \times 2 = 20$ points, $r = 1 \times 1 = 1$ point. Total = 117 points.

Maximum = $51 \times 5 = 255$ points, % abundance = $\frac{117}{255} \times 100 = 46$ approximately.

Table IV. *The fifteen worst weeds in relation to crops.*

| | Roots (100) | | | | | | | Wheat (39) | | | | | | | Oats (113) | | | | | | | Clover (50) | | | | | | |
|-----------------------|-------------|----|----|----|---|-----------|-----------|------------|----|----|----|---|-----------|-----------|------------|----|----|----|---|-----------|-----------|-------------|---|----|----|---|-----------|-----------|
| | D | s | f | o | r | % abd. | % abd. | D | s | f | o | r | % abd. | % abd. | D | s | f | o | r | % abd. | % abd. | D | s | f | o | r | % abd. | % abd. |
| Agrostis spp. | 0 | 5 | 28 | 35 | 0 | 35 | 0 | 0 | 0 | 5 | 16 | 0 | 24 | 0 | 4 | 1 | 25 | 41 | 1 | 32 | 0 | 3 | 0 | 7 | 20 | 0 | 30 | 0 |
| Atriplex patula | 5 | 5 | 10 | 19 | 4 | 23 | 0 | 2 | 1 | 2 | 10 | 1 | 21 | 0 | 4 | 7 | 9 | 19 | 2 | 20 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Cirsium arvense | 1 | 0 | 8 | 19 | 8 | 15 | 0 | 0 | 0 | 0 | 14 | 0 | 14 | 0 | 0 | 0 | 5 | 32 | 1 | 14 | 0 | 0 | 0 | 3 | 8 | 3 | 11 | 0 |
| Equisetum arvense | 12 | 4 | 22 | 36 | 0 | 43 | 0 | 1 | 0 | 9 | 23 | 0 | 40 | 0 | 4 | 1 | 11 | 49 | 0 | 27 | 0 | 0 | 0 | 6 | 17 | 2 | 22 | 0 |
| Galeopsis spp. | 0 | 0 | 7 | 20 | 5 | 13 | 0 | 0 | 2 | 5 | 21 | 0 | 33 | 0 | 2 | 2 | 16 | 42 | 4 | 27 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| Mentha arvensis | 1 | 3 | 16 | 14 | 0 | 19 | 0 | 0 | 0 | 7 | 9 | 0 | 20 | 0 | 0 | 1 | 24 | 26 | 0 | 23 | 0 | 0 | 0 | 2 | 8 | 0 | 9 | 0 |
| Poa annua | 0 | 0 | 15 | 21 | 0 | 17 | 0 | 7 | 2 | 13 | 14 | 0 | 56 | 0 | 0 | 1 | 8 | 44 | 0 | 21 | 0 | 9 | 2 | 21 | 6 | 0 | 51 | 0 |
| Polygonum aviculare | 1 | 4 | 5 | 48 | 1 | 27 | 0 | 1 | 0 | 3 | 30 | 0 | 38 | 0 | 2 | 1 | 7 | 51 | 0 | 24 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| Polygonum convolvulus | 0 | 0 | 4 | 34 | 8 | 18 | 0 | 0 | 0 | 3 | 22 | 0 | 27 | 0 | 0 | 0 | 12 | 62 | 2 | 29 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| Polygonum persicaria | 28 | 17 | 23 | 23 | 0 | 65 | 0 | 6 | 8 | 15 | 6 | 0 | 61 | 0 | 27 | 29 | 28 | 21 | 0 | 67 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Ranunculus repens | 3 | 3 | 10 | 31 | 1 | 24 | 0 | 0 | 0 | 1 | 20 | 1 | 23 | 0 | 3 | 1 | 9 | 30 | 0 | 19 | 0 | 2 | 0 | 15 | 23 | 1 | 41 | 0 |
| Rumex acetosella | 10 | 15 | 15 | 31 | 0 | 43 | 0 | 2 | 12 | 12 | 12 | 0 | 61 | 0 | 19 | 25 | 19 | 26 | 2 | 54 | 0 | 3 | 3 | 16 | 11 | 0 | 39 | 0 |
| Spergula spp. | 33 | 15 | 13 | 24 | 3 | 63 | 0 | 18 | 3 | 13 | 5 | 0 | 77 | 0 | 45 | 9 | 20 | 29 | 0 | 67 | 0 | 0 | 0 | 0 | 4 | 3 | 4 | 0 |
| Stellaria media | 13 | 6 | 10 | 37 | 1 | 39 | 0 | 4 | 3 | 12 | 12 | 1 | 48 | 0 | 5 | 7 | 32 | 41 | 0 | 41 | 0 | 0 | 0 | 0 | 5 | 0 | 4 | 0 |
| Viola spp. | 1 | 1 | 11 | 18 | 2 | 16 | 0 | 0 | 1 | 10 | 8 | 1 | 26 | 0 | 7 | 4 | 20 | 27 | 0 | 29 | 0 | 0 | 0 | 6 | 10 | 1 | 16 | 0 |

With corn-crops the case is different: there is here less opportunity for clearing the land and sometimes such weeds as spurry, sheep's sorrel and persicaria are rampant—smothering the crops. Autumn-sown crops like wheat have a greater percentage of weeds than spring-sown crops like oats.

Apart from the ordinary farming processes for the amelioration of the soil and the preparation of the ground for the reception of the crop—operations which in their nature tend to destroy the weeds—the question of the suppression or eradication of weeds is fundamentally bound up with the system of rotation, the scheme of drainage, and the application of manure (including liming). A simple farming process like hoeing by hand, which is resorted to in the case of certain weeds, is effective, and this accounts for the absence of such a weed as *Rumex crispus* from the tables of "worst weeds"; but for most weeds special means are necessary—means based on the study of the life-history of the plants concerned.

A study of the tables (III and IV) will show that *Rumex acetosella*, *Polygonum persicaria*, and *Spergula* spp., are outstanding from the points of view of frequency and abundance: speaking generally they are the *three* worst weeds in this district.

Polygonum persicaria grows on all soils, but is especially abundant on wet soils, and occurs amongst all crops except clover: *Rumex acetosella* is abundant on sour land—light, medium or peaty, and occurs amongst all crops: *Spergula* spp. grow in abundance on slightly or moderately acid soils—light, medium or peaty—and amongst all crops except clover.

These three weeds are closely followed in frequency, but not so closely in relative abundance, by *Equisetum arvense*, *Agrostis* spp., and *Stellaria media*: next come *Poa annua*, *Polygonum aviculare*, *Ranunculus repens*, and *Polygonum convolvulus*, of which *R. repens* is the most troublesome, especially on heavy land: *Viola* spp., *Galeopsis* spp., *Mentha arvensis*, *Atriplex patula*, and *Cirsium arvense* complete the list—the last-named being one of the most pernicious of all weeds; and on this account *C. arvense*, like *Rumex crispus*, which takes the next place, in frequency (Table V) is persistently attacked by the farmer. This factor—human activity—must be taken into account in estimating position on the list of "worst weeds."

Viola spp., which are abundant on peaty land, occur in two forms—*V. arvensis* and *V. tricolor*: on the "raw bog" the first form is the more frequent.

Galeopsis spp., also abundant on peaty land, occur in two forms—*G. speciosa* and *G. tetrahit*: these grow together but the former is the more frequent.

In the *Flora of Cheshire*, under the heading *Galeopsis versicolor*, the following passage occurs: "The Bee-nettle, as it is locally called, is perhaps the most characteristic plant of Central Cheshire. It evidently thins out towards the south and the sea. . . . The potato-fields, which it affects most, are often covered for roods with it. Curiously enough it is the commoner plant in my home

district than *G. tetrahit*, but there is plenty of the latter also, and they often grow together."

It is also called the "Dee nettle": in frequency and in relative abundance the order with crops appears to be wheat, oats, roots, clover.

Table V. *The "frequent" weeds in relation to soil.*

| Name | Times seen (max. 310) | Percentage frequency | | | | | No. of times dis- tributed | |
|------------------------|--------------------------------|----------------------|-------|--------|-------|---------------|-------------------------------------|------------|
| | | All soils | Heavy | Medium | Light | Silty peat | | Raw bog |
| Achillea millefolium | 7 | 2 | 0 | 6 | 0 | 4 | 0 | 1 |
| Achillea ptarmica | 20 | 6 | 0 | 13 | 5 | 2 | 0 | 2 |
| Agropyron repens | 10 | 3 | 2 | 2 | 3 | 5 | 0 | 1 |
| Arabis thaliana | 9 | 3 | 0 | 0 | 3 | 6 | 0 | 1 |
| Arrhenatherum bulbosum | 5 | 2 | 0 | 0 | 1 | 4 | 0 | 1 |
| Bellis perennis | 51 | 16 | 47 | 14 | 5 | 13 | 12 | 23 |
| Cerastium vulgatum | 56 | 18 | 49 | 12 | 7 | 16 | 18 | 4 |
| Crepis virens | 8 | 3 | 0 | 0 | 4 | 3 | 6 | 2 |
| Fumaria spp. | 64 | 21 | 0 | 20 | 18 | 35 | 12 | 5 |
| Geranium molle | 14 | 5 | 2 | 0 | 6 | 7 | 0 | 1 |
| Holcus mollis | 50 | 16 | 4 | 16 | 21 | 16 | 29 | 10 |
| Hypochoeris radicata | 11 | 4 | 0 | 2 | 7 | 4 | 0 | 1 |
| Lathyrus pratensis | 27 | 9 | 29 | 8 | 0 | 8 | 0 | 2 |
| Lotus spp. | 29 | 9 | 4 | 14 | 3 | 15 | 12 | 1 |
| Myosotis arvensis | 10 | 3 | 4 | 0 | 1 | 6 | 6 | 2 |
| Polygonum convolvulus | 153 | 49 | 35 | 40 | 51 | 64 | 29 | 17 |
| Polygonum hydropiper | 9 | 3 | 0 | 6 | 1 | 5 | 0 | 3 |
| Potentilla anserina | 28 | 9 | 6 | 2 | 1 | 23 | 0 | 1 |
| Prunella vulgaris | 34 | 11 | 33 | 10 | 4 | 7 | 6 | 3 |
| Rumex crispus | 97 | 31 | 59 | 16 | 11 | 45 | 24 | 4 |
| Sagina procumbens | 47 | 15 | 31 | 16 | 2 | 14 | 35 | 13 |
| Sonchus arvensis | 43 | 14 | 2 | 6 | 10 | 30 | 0 | 3 |
| Stachys palustris | 51 | 16 | 2 | 2 | 9 | 37 | 24 | 4 |
| Tussilago farfara | 59 | 19 | 0 | 20 | 12 | 8 | 0 | 2 |
| Veronica arvensis | 6 | 2 | 0 | 0 | 0 | 6 | 0 | 1 |
| Veronica hederacfolia | 14 | 5 | 0 | 0 | 8 | 5 | 12 | 1 |
| Vicia cracca | 33 | 11 | 12 | 6 | 12 | 13 | 0 | 2 |
| Vicia sepium | 53 | 17 | 4 | 0 | 13 | 39 | 0 | 9 |

All the weeds in these tables (V and VI) were in sufficient quantities, at least once, to be designated "frequent"; some of them, as for instance the scutchers or twitches (*Agropyron repens*, *Arrhenatherum bulbosum*, *Holcus mollis*), *Rumex crispus* and *Tussilago farfara* rank as the most harmful of all weeds and but for the persistent biotic attack would often attain a position of dominance; but most of the others rarely occur in sufficient numbers to have a harmful effect on the crops, either because they are intolerant of the measures adopted by the farmer for the prevention or suppression of weeds or because they fail in competition with other weeds or with the crops.

Arabis thaliana occurred chiefly amongst wheat on light sandy soil or on silty peat.

Polygonum hydropiper hardly ranks as an arable weed on land in good condition: it occurred on low-lying badly-drained areas on the silty peat of the moss-margin or on medium soil resting on a layer of impervious sub-soil.

Table VI. *The "frequent" weeds in relation to crops.*

| Name | Times seen (max. 302) | Percentage frequency | | | | |
|-------------------------------|-----------------------------|----------------------|-------|------|-------|--------|
| | | All crops | Wheat | Oats | Roots | Clover |
| <i>Achillea millefolium</i> | 7 | 2 | 8 | 2 | 2 | 0 |
| <i>Achillea ptarmica</i> | 20 | 7 | 8 | 3 | 14 | 0 |
| <i>Agropyron repens</i> | 9 | 3 | 0 | 4 | 5 | 0 |
| <i>Arabis thaliana</i> | 9 | 3 | 18 | 2 | 0 | 0 |
| <i>Arrhenatherum bulbosum</i> | 5 | 2 | 3 | 1 | 1 | 4 |
| <i>Bellis perennis</i> | 51 | 17 | 5 | 29 | 5 | 22 |
| <i>Cerastium vulgatum</i> | 56 | 19 | 18 | 12 | 11 | 48 |
| <i>Crepis virens</i> | 8 | 3 | 0 | 2 | 3 | 6 |
| <i>Fumaria</i> spp. | 60 | 20 | 31 | 16 | 21 | 10 |
| <i>Geranium molle</i> | 14 | 5 | 8 | 0 | 6 | 10 |
| <i>Holcus mollis</i> | 49 | 16 | 15 | 14 | 23 | 8 |
| <i>Hypochoeris radicata</i> | 11 | 4 | 3 | 3 | 2 | 10 |
| <i>Lathyrus pratensis</i> | 27 | 9 | 5 | 4 | 7 | 26 |
| <i>Lotus</i> spp. | 29 | 10 | 5 | 11 | 7 | 11 |
| <i>Myosotis arvensis</i> | 10 | 3 | 5 | 4 | 2 | 4 |
| <i>Polygonum convolvulus</i> | 148 | 49 | 64 | 67 | 46 | 2 |
| <i>Polygonum hydropiper</i> | 9 | 3 | 5 | 4 | 3 | 0 |
| <i>Potentilla anserina</i> | 27 | 9 | 13 | 12 | 5 | 6 |
| <i>Prunella vulgaris</i> | 34 | 11 | 5 | 10 | 9 | 24 |
| <i>Rumex crispus</i> | 97 | 32 | 38 | 37 | 21 | 38 |
| <i>Sagina procumbens</i> | 46 | 15 | 10 | 11 | 6 | 48 |
| <i>Sonchus arvensis</i> | 42 | 14 | 23 | 11 | 15 | 12 |
| <i>Stachys palustris</i> | 49 | 16 | 23 | 16 | 22 | 0 |
| <i>Tussilago farfara</i> | 58 | 19 | 44 | 20 | 12 | 12 |
| <i>Veronica arvensis</i> | 6 | 2 | 5 | 0 | 2 | 4 |
| <i>Veronica hederæfolia</i> | 14 | 5 | 13 | 6 | 1 | 2 |
| <i>Vicia cracca</i> | 32 | 11 | 13 | 14 | 4 | 14 |
| <i>Vicia sepium</i> | 53 | 18 | 23 | 6 | 13 | 42 |

Stachys palustris was found in fair quantities on wet land, more especially on the moss-margin at Warburton. In Ireland¹ it is an extremely common weed of arable land.

Table VII. *"Occasional" and "scarce" weeds.*

| | |
|-----------------------------------|--------------------------------|
| <i>Alchemilla arvensis</i> | <i>Lychnis alba</i> |
| <i>Brassica adpressa</i> | <i>Lychnis dioica</i> |
| <i>Brassica oleracea</i> | <i>Lythrum salicaria</i> |
| <i>Bromus arvensis</i> | <i>Matricaria chamomilla</i> |
| <i>Bromus mollis</i> | <i>Matricaria inodora</i> |
| <i>Cardamine flexuosa</i> | <i>Poa fluitans</i> |
| <i>Cardamine hirsuta</i> | <i>Polygonum lapathifolium</i> |
| <i>Chrysanthemum leucanthemum</i> | <i>Pteris aquilina</i> |
| <i>Digitalis purpurea</i> | <i>Raphanus raphanistrum</i> |
| <i>Erysimum cheiranthoides</i> | <i>Rhinanthus crista-galli</i> |
| <i>Euphorbia helioscopia</i> | <i>Rumex acetosa</i> |
| <i>Euphrasia officinalis</i> | <i>Rumex obtusifolius</i> |
| <i>Festuca bromoides</i> | <i>Scleranthus annuus</i> |
| <i>Festuca elatior</i> | <i>Sisymbrium officinale</i> |
| <i>Galium aparine</i> | <i>Taraxacum vulgare</i> |
| <i>Geranium dissectum</i> | <i>Thlaspi arvense</i> |
| <i>Heracleum sphondylium</i> | <i>Trifolium repens</i> |
| <i>Hypericum humifusum</i> | <i>Urtica dioica</i> |
| <i>Juncus communis</i> | <i>Veronica serpyllifolia</i> |
| <i>Lamium purpurea</i> | <i>Veronica tournifortii</i> |
| <i>Lapsana communis</i> | |

¹ Robert Lloyd Praeger, *Weeds*.

This list of weeds may be divided into two broad classes: those that are not strictly arable weeds but occasionally invade the arable land from waste land and hedges; and those that are usually regarded as arable weeds but for some reason or other rarely occur in abundance. To the first class belong such weeds as *Cardamine flexuosa* and *Heracleum sphondylium*, or weeds like *Digitalis purpurea*, *Juncus communis*, *Pteridium aquilinum* and *Poa (Glyceria) frutans*, which occur on very bad spots but which have no right, so to speak, to be on arable land at all: to the second class belong weeds, like *Galium aparine*, that are often present but rarely in any quantity, those like *Raphanus raphanistrum*, *Matricaria inodora*, and *Chrysanthemum leucanthemum*, which may be scattered thinly or which attain a position of dominance in small parts of the field, and those like *Scleranthus annuus* or *Matricaria chamomilla*, which are local in their distribution in the county area.

Matricaria chamomilla is common on arable land at Rostherne, near gates in particular, but sometimes it invades the inner parts of the field.

Thlaspi arvense is rare, occurring sometimes near gates, and is probably carried in manure: it was once found dominant on a small plot of oats on the edge of Carrington Moss.

Chrysanthemum leucanthemum was occasional, chiefly with "clover," but *C. segetum* was not seen once during the survey. This plant is recorded as "rather local" (F.C.)¹, "infrequent" (F.W.Y.) and "frequent in the west; rarer in the east and north" (F.W.L.).

¹ The records for these six weeds (page 394) in *The Flora of West Lancashire* by Wheldon and Wilson, 1907 (F.W.L.), in *The Flora of Cheshire* by Lord de Tabley, 1899 (F.C.), and in *The Flora of West Yorkshire* by Lees, 1888 (F.W.Y.), are as follows:

Convolvulus arvensis:

"Rather rare, and in the East almost unknown" (F.W.L.).

"Rare inland" (F.C.).

"Distribution peculiar; no record for districts Lune, Ribble or Mersey, i.e. none of the western river basins (F.W.Y.).

Linaria vulgaris:

"Frequent in the low country; very rare in the hilly districts" (F.W.L.).

"In hedges and about the borders of fields; also on sandy wastes near to the coast" (F.C.).

"Distribution nearly general; but no record at all for it in the basins of the Mersey tributaries" (F.W.Y.).

Plantago media:

"Common on limestone, rare elsewhere" (F.W.L.).

"A rare and local plant" (F.C.).

"Distribution nearly general—every district except Mersey" (F.W.Y.).

Papaver rhæas:

"Rather frequent in the North and West, especially in the tracts nearest the sea; rare elsewhere" (F.W.L.).

"Local and unequal distribution—chiefly shore" (F.C.).

"In Mersey, Lune, and elevated districts, sporadic and fugitive" (F.W.Y.).

Alopecurus agrestis:

"Very rare" (F.W.L.).

"An accidental introduction amongst sown grasses and grain crops, and not established with us" (F.C.).

"Colonist: corn- and clover-fields, rather rare (fortunately)" (F.W.Y.).

Urtica urens:

"Native; waste ground by barns and villages, fields (more rarely), infrequent, and nowhere in great quantity" (F.W.Y.).

"In garden ground, and about farmyards and roadsides, and wastes near dwellings, becoming in light sandy districts an agricultural weed" (F.C.).

"Frequent, but much less common than the preceding (*U. dioica*)" (F.W.L.).

Raphanus raphanistrum was found fully dominant in an oat field (not included in this survey) on the moss-margin at Warburton.

In a table¹ showing the varying habitats attributed to certain weeds by Buckman (1855), by Long (1910), and by Brenchley (1910-15) the following 15 weeds are taken as examples: *Alchemilla arvensis*, *Alopecurus agrestis*, *Convolvulus arvensis*, *Equisetum arvense*, *Galium aparine*, *Geranium dissectum*, *Linaria vulgaris*, *Lychnis vespertina*, *Papaver rhoeas*, *Plantago media*, *Ranunculus arvensis*, *Rumex acetosella*, *Scandix pecten*, *Spergula arvensis*, and *Urtica urens*. Dr Brenchley remarks: "In a few cases the differences between the tables are caused by the local distribution of certain weeds. If plants are at all localised it is quite likely that utterly different results may be obtained by various workers or by the same worker in different areas."

Only three of these weeds, *Spergula arvensis*, *Rumex acetosella* and *Equisetum arvense*, are to be found in any quantity in this area; six of them—*Alchemilla arvensis*, *Galium aparine*, *Geranium dissectum*, *Melandrium album* (*Lychnis vespertina*), *Scandix pecten*, and *Ranunculus arvensis*—are "rare"; and the remaining six² are not recorded at all from the land under observation. The following passage from Lord de Tabley's *Flora of Cheshire* may be of interest: "The Mosses of Bucklow (the Bucklow Hundred, in which the Altrincham 'local area' lies, was one of the seven Hundreds of Cheshire) are characterised notably by *Andromeda* and *Drosera anglica*; more locally by *Carex curta*, *elongata*, and *limosa*. The fields of root-crops are seldom without *Galeopsis versicolor* and *Fumaria Boraei*. The cereal crops, as compared with south England, have little variety of weed-flora. *Ranunculus arvensis*, *Scandix pecten*, *Alopecurus agrestis* are all absent or very rare. A poppy of any kind is in Bucklow a rarity."

NOTES ON *SPERGULA* SPP.

In the course of the study of the weeds of arable land special attention was directed to the genus *Spergula* in order to determine the relative abundance of its two recognised forms—*S. sativa* and *S. arvensis*—on the different types of soil within this area.

At the outset it was assumed that the papillae on the testa of the seed of one of these forms (*arvensis*) were a character of specific value giving that form a rank specifically distinct from the form (*sativa*) with non-papillate seeds. This assumption was based on the conclusion drawn from a small cultural experiment on *Spergula*³.

Over 5000 plants were examined in all, chiefly in the field with the aid of a pocket lens, and the chief results obtained are tabulated on p. 395.

The method adopted in all the cases tabulated below, was to pick, at random, individual plants all over an area where the soil was more or less uniform. In some other cases *handfuls* of plants were taken, but the results, though varying

¹ W. E. Brenchley, *Weeds of the Farmland*.

² See foot-note, p. 393.

³ Griffiths, 1922.

in the different handfuls, were similar to the others in the aggregate. Thus, on sandy loam near the edge of Carrington Moss 11 handfuls were as follows (*s* = *sativa*, *a* = *arvensis*): 44s 5a, 41s 5a, 28s 9a, 24s 9a, 31s 18a, 49s 1a, 13s 17a, 41s 31a, 21s 19a, 11s 12a, 60s 31a. This gives a total of 363 *sativa* to 157 *arvensis*—an approximate ratio for the whole of about 2·3 : 1.

| Locality | Geological formation | Soil | No. of plants examined | | Approx. ratio |
|--------------|----------------------|-----------------------|------------------------|-----------------|---------------|
| | | | <i>sativa</i> | <i>arvensis</i> | |
| Warburton | Peat moss | Acid peat | 515 | 114 | 4·5 : 1 |
| | Moss-margin | Peaty | 592 | 99 | 6·0 : 1 |
| | Moss-margin | Silty peat | 165 | 35 | 4·7 : 1 |
| | Post-glacial sands | Dark sandy loam | 225 | 83 | 2·7 : 1 |
| | Post-glacial sands | Light loam | 188 | 179 | 1·1 : 1 |
| Rostherne | Glacial sands | Light loam | 347 | 369 | 0·9 : 1 |
| | Glacial clays | Medium loam | 590 | 378 | 1·6 : 1 |
| | Glacial clays | Moderately heavy loam | 283 | 108 | 2·6 : 1 |
| Castle Mills | Glacial sands | Light to medium loam | 242 | 152 | 1·6 : 1 |
| | Glacial clays | Medium to heavy loam | 274 | 46 | 6·0 : 1 |

For purposes of comparison with Warburton Moss a few plants were picked at random from Carrington Moss and the results worked out at about 7s to 1a: near the moss-margin, on sandy loam, the results were approximately 2s to 1a.

On farms situated on the northern flanks of Cader Idris (Dolgelley, Merioneth) in fields of medium stony loam both forms were present with *S. sativa* greatly predominating: out of 498 plants examined 452 were *S. sativa* and 46 *S. arvenis*, giving an approximate ratio of 9·8 : 1¹.

On light or medium loamy soil, slightly acid in reaction, *Spergula* is often rampant: such soils, especially if the sub-soil tends to be impervious to water, seem to be an ideal habitat, and the two forms occur in more or less equal proportions. Should these conditions vary—should the soil become heavier or more acid, for instance—the plant becomes less plentiful and *sativa* the dominant form.

On very heavy soil *Spergula* is usually scarce, say one or two plants to about 10 acres of land, or absent; but in one case, on a dump of stiff clay, the plant was present in fair numbers. These were all *sativa* forms and incidentally remarkable for their branching and spreading habits².

On acid peat, where *Spergula* cannot be said to be usually abundant though often frequent, and on the less acid but silty peat of the damper moss-margins, where it is abundant and often dominant, the characteristic form is *sativa*.

¹ This district is left blank on the map showing the relative distribution of the two forms in Great Britain (*Cambridge Flora*): for other parts of North Wales *sativa* only is denoted. Mr C. E. Salmon, writes: "I believe *sativa* to be the more common species in Great Britain both in numbers and distribution; it is certainly more widely spread in Scotland and occurs there in many more counties than *arvensis*. It may be a more northern form."

² On the more heavy land, in general, *Spergula* appears to assume a more branching and spreading habit.

Though only "occasional" on a field in general *Spergula* was often observed to be dominant round the periphery (say about five yards into the field from the edge). This may indicate that the plant is intolerant of overcrowding or of lack of light and suggests the growing of "smothering" crops as an effective counter-measure.

Though special attention was directed only to the question of the distribution and the relative abundance of these two species the following observations may be of some interest if only in calling attention to the variable character of this plant.

Despite variations in the form, size, colour and viscosity of the shoots, in the number of stamens, and in the shape of the capsules, it cannot be said, as far as the writer's experience goes, that there is present any character sufficiently distinct and constant by which *S. sativa* may be distinguished from *S. arvensis* at a glance¹.

S. sativa may be, on the whole, of a dull green as against the yellowish green colour of *S. arvensis*; yet plants were found growing together that showed no appreciable difference in this respect: most observers regard the *arvensis* form as the more viscid; yet plants were found on the same ground in which this state of affairs was reversed: the wing on the seed is also a very variable character; sometimes it may be almost absent in both forms, sometimes larger in *arvensis* than in *sativa* and vice versa: the number of stamens may vary in both forms from 5 to 10—the variability being due chiefly to the incompleteness of the outer ring: the seed-coats darken with age and when the seed is mature the prevailing colour is dark brown or black: the papillae on the seed-coats also may darken with age² and they often vary from grey or light brown to very dark brown (almost black) on the same seeds; but again black, apparently mature, seeds with grey papillae were common: in some cases very few papillae were present and in others they occurred in patches leaving surfaces uncovered which could not be distinguished from the surface of seeds without papillae; but in no case were seeds with papillae found in the same capsule, or on the same plant but in different capsules, as those with non-papillate seeds³.

To sum up: *Spergula sativa* and *S. arvensis* both occur in this district; but *S. sativa* is the dominant or characteristic form. They are often abundant

¹ Cf. **Nicholson**, 1880: "Although when growing, so far as my experience goes, *S. sativa* and *S. vulgaris* are quite distinct and can be easily recognised, their differences seem to disappear when dried, and the only reliable characters are in the mature seed." And again cf. **Druce**, 1891: "When growing in dry, sandy soil, *S. sativa* may be distinguished from *S. vulgaris* by the more viscid pubescence with which it is clothed, and by the duller and more yellowish green of the former plant."

² **Druce**, 1891.

³ Cf. **Moss** (*Cambridge Flora*): "This variety (i.e. *S. arvensis* var. *vulgaris*) seems to hybridise with the var. *sativa*, for plants with mixed characters occur (e.g. in Cambridgeshire) when the two grow together."

and nearly equally distributed on light or medium loamy soils slightly acid in reaction: on peaty or on medium to heavy soils *S. sativa* predominates: on very heavy land the plant is almost absent. There seems to be present no character by which the species may be readily distinguished from one another except by examination of the seeds: no forms which could *definitely* be termed intermediate or hybrid were found¹.

SUMMARY.

In the preceding pages an attempt has been made to give (1) a general account of the geology of the Cheshire Plain—more especially of the geology of its superficial deposits in virtue of their direct bearing on the vegetation; (2) a general account of the topography of the Altrincham "local area" with a more or less detailed account of some semi-natural plant communities on peaty soil; (3) a general account of agricultural practice and procedure on certain farms within this "local area," with a detailed account of the weeds of arable land on those farms—a part of a wider scheme of weed survey²; and (4) some notes, the results of more or less casual observations on the plant *Spergula*, with special reference to the relative abundance of its two chief forms, *S. arvensis* and *S. sativa* on the different types of soil within the area.

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For permission to go on to the fields and for information concerning rotation, manure, etc., I am indebted to Mr John Pennington, Dunham Massey (and through him to Mr Samuel Pennington), to Mr Jones, Yew Tree Farm, and to Mr Beckett (also to Mr J. Beckett, Jun.), Carr Green, Warburton, to Mr Pimlott, Denfield Hall, Rostherne, to Mr J. Newton, Homestead, Millington, and to the late Mr T. Merrell, Castle Hill Farm, Castle Mills.

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¹ It seems clear that *Spergula* and its forms deserve more serious attention from the expert systematist; but owing to the difficulty of distinguishing these forms *in the field at a glance*, as far as the practical agriculturist is concerned no useful purpose seems to be served by separating them, and on that account all the observations in the tables are grouped under the heading *Spergula* spp.

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NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

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THE present series of notices (together with those published in the last number of *The Journal of Ecology*) covers about fifty smaller and twenty larger journals in which ecological material is liable to be published, and includes the period between January 1926 and December 1927. The fifty smaller ones include all the more important regional natural history journals of the type of the *Scottish Naturalist*; a number of *Proceedings* or *Transactions* or *Annual Reports* of local societies, of which a good many are, however, either unobtainable in libraries, or else contain little in the way of records; and also a certain number of journals like the *Journal of Conchology* and *British Birds*. The larger group comprises most of the well-known zoological journals, together with some others.

The *Entomologist*, the *Entomologist's Monthly Magazine*, and the *Field*, have not been covered, the last because of its diffuseness and size, and the former chiefly because the observations published are in any case brought into circulation more naturally through the medium of text-books on insect groups. All three contain scattered ecological notes.

The impression gained by looking through all the smaller natural history journals is that it would be a great blessing if groups of local societies combined more frequently to produce one single journal dealing with each region, thus pooling all their observations. This has been done in some places with great success. Unless it is done, the published results tend to be meagre (on account of expense) and poor in quality (owing to the fact that they are unlikely to be read at all widely). In spite of this, however, the amount of useful work published by them is rather greater than might be expected.

Another fact that strikes the reader of these small journals is that most of the best regional journals are associated directly or indirectly with some university or some big museum. This points to an obvious and useful development in the future.

A very interesting joint paper by R. Gurney, F. W. Oliver, E. J. Salisbury, and T. C. Blofield has recently been published (in the *Trans. Norfolk and Norwich Nat. Soc.* **12**, pp. 307-316, 1926-27) under the title of "The functions of a local natural history society." This contains a number of useful ideas, and suggests various examples of the type of ecological and other work which may be undertaken by local societies.

1. GENERAL PAPERS ON PARTICULAR GROUPS OF ANIMALS.

Green, E. E. "Notes on the Coccidae of Scotland." *Scottish Nat.* 1927, pp. 25-30, 55-59.

Notes on the occurrence and distribution, with a few data on habitats.

Chrystal, R. N. "The Genus *Dreyfusia* (Order Hemiptera, Family Chermesidae) in Britain, and its Relation to the Silver Fir." *Phil. Trans. Royal Soc. (London)*, **214**, pp. 29-61. 1926.

Stelfox, A. W. "A list of Hymenoptera Aculeata (*sensu lato*) of Ireland." *Proc. Royal Irish Acad.* **37**, Sect. B, pp. 201-355. 1927.

An important account, which includes the Chrysididae and Bethyridae, as well as the Ants, Bees, and Wasps. Contains numerous valuable notes on the distribution and ecology of the various species, together with a large bibliography.

Pack-Beresford, D. R. "A List of the Harvest-Spiders of Ireland." *Proc. Royal Irish Acad.* **37**, Sect. B, pp. 125-140. 1926.

This account contains very few ecological data, but gives the general distribution of the species, together with a good bibliography, which apparently includes most of the literature relating to Britain.

Friend, H. "The *Eisenias* of North Wales." *North Western Nat.* **2**, pp. 7-8. 1927.

Notes on this genus of earthworms, mostly descriptive of their specific characters.

Hurrell, H. E. "The Ecology of the Fresh-Water Polyzoa in East Anglia." *Journ. Royal Microsc. Soc.* **47**, pp. 135-142. 1927.

A general account, with notes on habitats of some species and on methods of studying them.

2. ECOLOGICAL SURVEYS AND HABITAT NOTES.

Light, S. S. "The Fauna and Flora of Apple Bark." *Ann. and Mag. of Nat. Hist.* **17**, pp. 126-149. 1926.

An important account, based on work done in the Bristol district. All the species of insects are listed (including those found hibernating under bark in winter), but only a few of the spiders, mites, myriapoda, and woodlice. Amongst the plants growing on the bark, all are listed except Fungi. The author mentions that trees sprayed for the removal of scale in one place, were heavily infested with the scale later on; whereas the opposite was the case in trees that were not sprayed. This was apparently due to the destruction by the spray of certain mites which eat scales, while on the unsprayed trees the mites survived and kept the scales in check.

Barnes, H. F. "The Crane-flies of Carnarvonshire." *North Western Nat.* **1**, pp. 17-34. 1926.

A complete list, with notes on the habitats, distribution and seasonal occurrence of each species. Some additional notes are given by Wallace, C. H., in the same journal, **1**, p. 83, 1926, and **2**, p. 98, 1927.

Womersley, H. "Collembola." *Rept. of the Marlborough College Nat. Hist. Soc.* for 1926, No. 75, pp. 39-40. 1927.

A list of springtails found in Savernake Forest, giving the habitats in some cases.

Anon. "Oxshott Visit, April 18th, 1925." *Proc. South London Entom. and Nat. Hist. Soc.* 1926, p. 64.

Records of certain species of insects are given, together with notes on their habitats. References are given to previous notes on Oxshott Common in the same journal. More notes are given in the *Proc.* for 1927, pp. 104-105.

Dallman, A. A. "*Sepsis cyanea* L." *North Western Nat.* 2, p. 28. 1927.

Very abundant in one place, Sept. 1926; seen pollinating flowers of *Tussilago farfara* earlier in the season.

Williams, B. S. "A Further List of Species of Coleoptera new to the County of Hertfordshire." *Trans. Hertfordshire Nat. Hist. Soc. and Field Club*, 18, pp. 172-176. 1927.

Gives the habitats of many of the species of beetles collected, e.g. from nests of the ant, *Lasius fuliginosus*, from nest of starling and of mole, from *Sphagnum*, etc.

Britten, H. "An interesting Coleopteron breeding in the Goyt Valley." *North Western Nat.* 2, p. 177. 1927.

Hylecoetus dermestoides living in stumps of oak and beech.

Dallman, A. A. "Dipteran Visitors of *Angelica*." *North Western Nat.* 2, p. 180. 1927.

List of species found on *Angelica* flowers by the author.

Earl, H. L. *Trans. and Proc. Torquay Nat. Hist. Soc.* 5, pp. 75-76. 1926-27.

The parasitic bee *Nomada lathburiana* K. was found in large numbers near a colony of its host *Andrena cineraria*, at Newton Abbot, in April. It had never been found in this area during the previous 15 years, although searched for carefully. Various records of Phytophagous Hymenoptera and of Diptera are given, with habitat notes in some cases (e.g. pH of the water from which different species of mosquitoes were obtained). Similar notes in the same journal, 4, pp. 381-382, 1925-26.

Pearman, J. V. "Psocoptera." *Proc. Somersetshire Arch. and Nat. Hist. Soc.* for 1927, 13, p. lviii. 1928.

List of Psocids taken in Somerset, giving general habitat notes in some cases (e.g. "sandhills," "houses").

Richards, O. W. and **Robson, G. C.** "The Land and Freshwater Mollusca of the Scilly Isles and West Cornwall." *Proc. Zool. Soc. (London)*, 1926, pp. 1101-1124.

Contains a very careful analysis of the habitats of most of the species of molluscs, with notes on rock-types and plant association. Also a very useful general account of the Scilly Isles, from an ecological point of view.

Friend, H. "Annelid Hunting in North Wales." *North Western Nat.* 1, pp. 201-204. 1926.

Contains notes on species found near Colwyn Bay, with habitats.

Garnett, H. "Occurrence of *Rhynchodemus britannicus* Percival in Lancashire." *North Western Nat.* 1, p. 148. 1926.

A land flatworm, found attacking a worm on Heaton Moor.

Ritchie, John. "Survey of Methven Loch." *Trans. and Proc. Perthshire Soc. of Nat. Sci.* **8**, pp. 213-214. 1926-27.

Notes on a preliminary ecological survey, with a list of some of the animals (mollusca, leeches, worms, and bugs).

Gurney, R. "The Distribution of the Crayfish, *Potamobius Pallipes*, in Norfolk." *Trans. Norfolk and Norwich Nat. Soc.* **12**, pp. 261-262. 1925-26.

Notes some localities where it occurs.

Harris, G. T. "Fauna of Wells in Devonshire." *Trans. Devon. Ass. for Advancement of Sci., Lit. and Art*, **59**, p. 226. 1927.

The Isopod *Asellus meridionalis* was found living in a closed well nearly a hundred feet deep, in company with *Cyclops viridis*.

Lowndes, A. G. "Pond Life." *Rept. of the Marlborough College Nat. Hist. Soc.* for 1926, No. 75, pp. 69-72. 1927.

Notes on species of *Cyclops* and the pH of the water of their habitats. *C. languidus* was taken in a sphagnum pond full of *Leptothrix ochracea*. The Fairy-shrimp, *Chirocephalus diaphanus* occurs in ponds in Savernake Forest.

Lowndes, A. G. "*Attheyella wulmeri*, Kerhervé." *Rept. of the Marlborough College Nat. Hist. Soc.* for 1927, No. 76, pp. 69-73. 1928.

Useful description of this Harpacticid Copepod, which was found in spring in temporary waters, together with *Cyclops latipes* and *C. bisetosus*.

Popple, E. "Report on Hertfordshire Crustacea." *Trans. Hertfordshire Nat. Hist. Soc. and Field Club*, **18**, p. 164. 1927.

Some records of *Cyclops* from ponds, and of *Chirocephalus* from temporary pools.

Elmhirst, R. "Two Sand-dwelling Nemertine Worms new to Britain." *Scottish Nat.* 1926, pp. 93-94.

Lineus coccineus and *Amphiporus langiaegeminus* living in intertidal sand, on coast of Ayrshire.

Stephen, A. C. "Bivalves and Anemones on Whale's Skull." *Scottish Nat.* 1927, p. 24.

The rare bivalve, *Adula simpsoni*, has the curious habit of growing almost exclusively on the submerged skulls of whales.

3. ACTION OF ENVIRONMENTAL FACTORS.

Longstaff, T. G. "Local Changes in Distribution." *Ibis*, **2**, pp. 637-656. 1926.

An important account of the effects of ecological succession and of other factors, upon the numbers and composition of the bird fauna of a garden in the New Forest, between the years 1913 and 1925. The interplay between ecological succession of the vegetation on the one hand, and independent fluctuations in numbers of the birds on the other, is well brought out; and the relation of these points to migration is discussed.

Stewart, W. "Studies of some Lanarkshire Birds. The Jackdaw." *Scottish Nat.* 1927, pp. 149-156.

A good analysis of the variation in nesting habits. Formerly, the largest class was that nesting in trees. Now, about 35 per cent. are estimated to nest in rabbit burrows (both rabbits and jackdaws having increased in numbers). The jackdaw probably helps to spread a disease (parasitic scab) among the rabbits, by using the old skins of dead rabbits for nesting material. The type of tree-nest is also said to have changed in recent years.

Hellyar, R. H. "Notes on the Nesting of the Sand-Martin." *British Birds*, 21, pp. 166-171. 1927.

Contains an account of local changes in the type of nesting site chosen, and a discussion of the reasons for these changes.

Gemmell, J. F. "On the Life-History and Bionomics of the Wheat Bulb Fly (*Leptohylemyia coarctata* Fall.)." *Proc. Royal Physical Soc. Edinburgh*, 21, pp. 133-158. 1927.

Extensive notes on the ecology of this species; contains also a note on larvae of the fly, *Bibio lacteipennis* Ztt., attacking wheat.

Percival, E. and Whitehead, H. "Observations on the Biology of the Mayfly, *Ephemera danica*, Müll." *Proc. Leeds Phil. and Lit. Soc.* 1, pp. 136-147. 1926.

A study of the exact habitat of this insect, whose larva is shown to be confined to certain types of sandy bottoms in rivers. Analyses of the sand substratum are given, and many useful observations on the habits of the mayfly.

Boycott, A. E. "Land Snails at Nevin." *North Western Nat.* 2, pp. 238-241. 1927.

Lists from one or two habitats, with a discussion of the distribution (calicology, etc.) of certain species.

Boycott, A. E. "Oecological Notes, 7. *Margaritina margaritifera* in hard water." *Proc. Malacological Soc.* 17, p. 184. 1927.

It was thought that the pearl mussel only lived in soft water. This record from the River Nore in Ireland disproves the idea, and experiments by the author also show that the mussel can tolerate hard water. Other cases are mentioned of local variation in the calciculous habits of molluscs.

Walton, C. L. and Wright, W. R. "Hydrogen-ion Concentration and the Distribution of *Limnaea truncatula* and *L. peregra*, with a Note bearing on Mosquitoes." *Parasitology*, 18, pp. 363-367. 1926.

Evidence is given that these two snails do not actually live together, although they may inhabit the same piece of water. The different distribution is not due to differences in pH of the water (although the two species do have limits of tolerance to pH, e.g. *L. truncatula* pH 6-8.6, *L. peregra* pH 5.8-8.8). The determining factor is probably the softness of the muddy substratum. The authors point out that MacGregor's work, on tolerance limits of mosquito larvae to pH of water, is not supported by their field observations on mosquito larvae. *Aedes detritus* was kept successfully in water of pH 4.2.

Thorpe, W. H. "The Fauna of Brackish Pools of the Sussex Coast." *South-Eastern Nat.* 1927, pp. 27-34.

A preliminary account of the animals (insects, crustacea, worms, etc.) found in brackish pools in the neighbourhood of Rye, with notes on the salinities tolerated by certain species.

Russell, F. S. "The Vertical Distribution of Plankton in the Sea." *Biological Reviews (Cambridge Phil. Soc.)*, 2, pp. 213-262. 1927.

Complete summary and review of work on this subject, together with a large bibliography.

4. PARASITES OF ANIMALS.

Lewis, E. A. "A Survey of Welsh Helminthology." *Journ. Helminthology*, **5**, pp. 121-132. 1927.

Includes a list of parasitic worms collected by the author in the Aberystwyth area from birds and mammals, together with their host species, many of them wild animals. The main part of the paper deals with the history of work in Wales, mainly on domestic animals.

Lewis, E. A. "Starlings as Distributors of 'Gapes'." *Journ. Helminthology*, **4**, pp. 43-48. 1926.

Out of 482 starlings examined in winter, 169 (35 per cent.) were infested with the gape-worm *Syngamus trachealis*, which causes severe epidemics among young chickens, but does not attack adult fowls. It also attacks pheasants. The author gives evidence that the starling may act as an important agent in spreading and forming a reservoir for this round-worm.

Leiper, R. T. "Gapes." *Proc. Zool. Soc. (London)*, 1926, pp. 713-714.

Following the discovery of Lewis, mentioned above, Leiper has proved by experiment that the worm in starlings is indeed *Syngamus trachealis*, and is capable of producing the disease in poultry.

Lewis, E. A. "Helminths of Wild Birds found in the Aberystwyth Area." *Journ. Helminthology*, **4**, pp. 7-12. 1926.

Includes, among many others, some records of *Syngamus trachealis* from wild birds.

John, D. D. "On *Cittotaenia denticulata* (Rudolph 1804), with Notes as to the Occurrence of other Helminthic Parasites of Rabbits found in the Aberystwyth Area." *Parasitology*, **18**, pp. 436-454. 1926.

Study of the ecology of this tapeworm, with notes also on another species (*C. pectinata*). He obtained strong evidence that these two species never occurred together in the same individual rabbit. Larval tapeworms and some nematodes are noted; while *C. pectinata* was found in hares, also.

Ritchie, John. "Some Museum Notes." *Trans. and Proc. Perthshire Soc. of Nat. Sci.* **8**, pp. 211-213. 1926-27.

Contains records of parasites identified from various hosts: from red deer (flies); roedeer (tick); wild cat (nematode and tapeworm); pipistrelle (mite); brown lizard (nematode); quail (tapeworm); cuckoo (tapeworm); house martin (mite); and bloodsucking fly from nests of martin.

Slater, H. "Siphonaptera." *Proc. Somersetshire Arch. and Nat. Hist. Soc.* for 1926, **72**, p. lxviii. 1927.

List of fleas from various birds and mammals, including *Ceratophyllus gallinulae*, bred from nest of Red-Backed Shrike.

Perrens, C. J. "Ichneumonidae." *Proc. Somersetshire Arch. and Nat. Hist. Soc.* for 1926, **72**, p. lxvi. 1927.

Trogus lutorius bred from pupa of *Sphinx populi*, Bridgwater, 1926.

Slater, H. H. "Ichneumonidae." *Proc. Somersetshire Arch. and Nat. Hist. Soc.* for 1927, **73**, p. lx. 1928.

Records occurrence of *Rhyssa persuasoria* at Stoke St. Mary. This ichneumon parasitises the large wood-wasp, *Sirex gigas*, which was originally introduced in foreign timber.

Thomson, W. R. and Parker, H. L. "The Problem of Host Relations with Special Reference to Entomophagous Parasites." *Parasitology*, **19**, pp. 1-34. 1927.

An extremely important account of the manner in which certain polyphagous parasitic diptera and hymenoptera select their hosts. The authors believe that it is often almost impossible to predict, from the previous known habits of the parasite, how it will behave in contact with a possible new host.

Brown, F. J. "Some British Freshwater Larval Trematodes, with Contributions to their Life-Histories." *Parasitology*, **18**, pp. 21-34. 1926.

Many of these larvae were of doubtful status; they appear to pass through freshwater mollusca, and probably end up in ducks and other aquatic birds (although the final hosts are not yet known for certain).

Brown, F. J. "On *Crepidostomum farionis* (O. F. Müll.) (= *Stephanophiala laureata* Zeder), a Distome Parasite of the Trout and Grayling. 1. The Life History." *Parasitology*, **19**, pp. 86-99. 1927.

The larva of this worm is shown to pass first into molluscs (*Pisidium amnicum* and *Sphaerium corneum*), then into a mayfly (*Ephemera danica*), which is then eaten by Trout or Grayling, the worm reaching the adult condition in these fish.

Leigh-Sharpe, W. H. "A List of Parasitic Copepoda found at Plymouth." *Parasitology*, **18**, pp. 384-386. 1926.

The names of the hosts, and the parts of their bodies inhabited, are given.

5. PLANT GALLS.

Dallman, A. A. "*Mecinus collaris* Germ. in Lancashire." *North Western Nat.* **2**, pp. 256-257. 1927.

Galls on *Plantago maritima*, caused by this weevil.

Britten, H. "Galls of *Perrisia gallii* H. Low on Lady's Bedstraw, *Galium verum* L." *North Western Nat.* **1**, p. 213. 1926.

Falconer, W. "Report on Plant Galls for 1926." *North Western Nat.* **2**, pp. 178-179. 1927.

Chapman, V. J. and Hurst, C. P. "Plant Galls found in 1926." *Rept. of the Marlborough College Nat. Hist. Soc.* for 1926, No. 75, pp. 76-77. 1927.

Hurst, C. P. "Plant Galls." *Rept. of the Marlborough College Nat. Hist. Soc.* for 1927, No. 76, pp. 80-81. 1928.

Massee, A. M. "A Contribution to the Knowledge of the Species of Gall-Mites (Eryophyidae) of Sussex." *Ann. and Mag. Nat. Hist.* Ser. 9, **20**, pp. 375-379. 1927.

Hall, L. B. "Plant Galls of Hampshire and Dorset." *Proc. Bournemouth Nat. Science Soc.* **19**, pp. 56-58. 1927.

6. FOOD-HABITS.

Tucker, B. W. "Bird's-nesting Bank Voles." *British Birds*, **20**, pp. 158-160. 1926.

Evidence was given that bank voles destroy birds' eggs. This note was followed by a number of other communications by various authors, in the same journal (**20**, pp. 180-181, 198-199, 207, 230, 255), which showed that various species of mice commonly attack birds' eggs.

Wild, O. H. "Wasps destroying young Birds." *British Birds*, **20**, pp. 254-255. 1927.

Longstaff, T. G. "Bird's-nesting Mice and Insects." *British Birds*, **20**, pp. 198-199. 1927.

Notes certain insects (e.g. ants) attacking nestlings, and mice destroying eggs.

Patterson, A. H. "Bird Notes 1923-26." *Trans. Norfolk and Norwich Nat. Soc.* **12**, pp. 299-303. 1926-27.

Includes observations on the food-habits of various birds: Rooks (feeding young on stranded marine Crustacea); Starlings and Sparrows (eating sea-shrimps); Black-throated Diver (Bream and Smelt); Little Owl (Cockchafers, Rose-chafers, and other beetles, also Pigmy Shrew, and Bats); Bittern (young Warblers); Kestrel attacking Dunlin; Starlings and Rooks eating walnuts. The author noted that a Natterjack Toad rejected Cinnabar caterpillars; while a Kestrel rejected a Natterjack, which was offered to it.

Betts, E. St G. "Tawny Owls and Batrachian Food." *British Birds*, **21**, p. 41. 1927.

Discussion of food of this owl; rats are an important item, as also are frogs or toads (uncertain which), whose bones were commonly found in owl pellets by the author.

Wenner, M. V. "Sparrowhawk capturing a Bat." *British Birds*, **21**, p. 17. 1927.

Collinge, W. E. "Some Remarks upon the Insect Food of the Black-headed Gull (*Larus ridibundus* L.)." *Ibis*, **3**, pp. 196-201. 1927.

Most of the birds examined were from Scotland. The percentage of insects was high (from 10 per cent. to 54 per cent., average 24.70 per cent., based on examination of 644 stomachs); a list of the species is given.

Allen, F. "Food of Black-headed Gull and other Birds." *North Western Nat.* **2**, p. 94. 1927.

Stomach of one gull contained masses of a *Corixa* (*Glaenocorisa cavifrons*). Also notes a Kestrel eating a Pigmy Shrew; and Starlings eating pupae of a fly (*Oligotrophus ventricolus*) living in *Molinia* tussocks.

Patterson, A. H. "Food of the Sturgeon." *Trans. Norfolk and Norwich Nat. Soc.* **12**, pp. 380-381. 1926-27.

Stomach of one contained about 729 small fish (lesser sandlaunces).

Forrest, H. E. "Fishes." *Caradoc and Severn Valley Field Club, Record of Bare Facts for the Year 1926*, p. 19, 1927.

Stomach of an eel (*Anguilla vulgaris*) from the Severn was full of small bivalves (*Sphaerium corneum*).

Elmhirst, R. "Notes on Fishes from the Firth of Clyde." *Scottish Nat.* 1926, pp. 151-158 and 179-186.

Includes analyses of stomach contents of cod (p. 157) caught round the Cumbræes (Ayrshire Coast). The species of food-animal are given in many cases.

Cuthbertson, A. "The Trout as a Natural Enemy of Crane-Flies." *Scottish Nat.* 1926, pp. 85-88.

Contains (a) lists of insects (not only flies) found in the stomachs of trout, and (b) field notes on species of flies found near the water (based, in some cases, on rearing of the larvae).

Cuthbertson, A. "Spiders as Enemies of Crane-Flies." *Scottish Nat.* 1926, pp. 127-129.

List of species which eat Crane-Flies, of which the species are given. Special study of the preys found in webs of the wood-spiders, *Zilla atrica* and *Z. x-notata*.

Blair, W. N. "Notes on *Hirudo medicinalis*, the Medicinal Leech, as a British Species." *Proc. Zool. Soc.* (London), 1927, pp. 999-1002.

This leech, thought to be almost extinct in England, is still very numerous in ponds in the New Forest, where the larvae live on frog-tadpoles and fish, and the adults on horses and cattle. Interesting observations on the habits.

Oldham, J. N. "On the Larval Stage of *Pedicia rivosa* L." *Proc. Royal Physical Soc. Edinburgh*, **21**, pp. 33-63. 1926.

This is a Limnobiid fly, whose larvae live in streams and are carnivorous, eating the larvae of other small insects. These notes relate to streams in Argyllshire.

Keilin, D. "Fauna of a Horse-Chestnut Tree (*Aesculus hippocastanus*). Dipterous Larvae and their Parasites." *Parasitology*, **19**, pp. 368-374. 1927.

An interesting account of a miniature community living in and around the edge of a natural water-hole in a tree. Sap-exudations or slime-fluxes were associated with it also. The water was alkaline. The food habits of the larvae are given, and an account of various bacteria, protozoa, and fungi parasitic on and in them.

Britten, H. "Dragonflies on a Westmorland Moss." *North Western Nat.* **2**, pp. 27-28. 1927.

A short list of species observed on Cliburn Moss, June 1926, with notes on their habits. *Corduligaster annulatus* was seen hawking for insects over young pines, in company with swallows and martins; *Lestes sponsa* was seen catching small moths among the heather.

Smith, K. M. "A Study of *Hylemyia* (*Chortophila*) *brassicæ* Bouché, the Cabbage Root Fly, and its Parasites. With Notes on some other Dipterous Pests of Cruciferous Plants." *Ann. Applied Biol.* **14**, pp. 312-330. 1927.

Description of life-history, enemies, and parasites. The larvae of a small beetle (*Aleochara bilineata*) destroy the pupae of the fly; while a Cynipid and a Braconid parasitise the larvae, which are also eaten by the carnivorous larva of an Anthomyid fly. The larva of the beetle is itself parasitised by a Proctotrupid.

James, H. C. "The Life-History and Bionomics of a British Phytophagous Chalcidoid of the Genus *Harmolita* (*Isosoma*)." *Ann. Applied Biol.* **14**, pp. 132-149. 1927.

Many species of this genus are pests on cereals and cultivated grasses. The life-histories of the species forming galls on couch grass (*Triticum repens*) were studied. A Braconid parasitises the larvae, while "large numbers of larvae are pecked out of galls by birds, particularly by tits; especially if the winter is severe" (p. 147).

Britten, H. "Red Ants and Beetles." *North Western Nat.* **2**, p. 256. 1927.

Myrmica ruginodis killing beetles (*Melandrya caraboides*) which had bored into decaying logs of ash. Also notes, made at various times, on beetles and flies living in the same decaying logs.

Britten, H. "Ants and Sundews." *North Western Nat.* **1**, pp. 37-38. 1926.

Myrmica laevinodis carrying away insects (butterflies, dragonflies, etc.) which had been caught by sundews (*Drosera rotundifolia*). The ants were doing this on a large scale in the area studied.

Britten, H. "A Pentatomid Bug preying on Beetle Larvae." *North Western Nat.* **1**, p. 38. 1926.

Rhacognathus punctatus found sucking larvae of beetle (*Hydrothassa marginella*) which was feeding in numbers on *Caltha palustris*.

Britten, H. "*Dicyphus stachydis* Reut. feeding on *Heracleum Sphondylium* L." *North Western Nat.* **1**, pp. 212-213. 1926.

A Capsid bug, which usually feeds on *Stachys sylvatica*.

Dallman, A. A. "An Aphid Note." *North Western Nat.* **1**, p. 40. 1926.

Macrosiphum epilobiellum on *Epilobium montanum* in Derbyshire.

Smith, K. M. "Observations on the Insect Carriers of Mosaic Disease of the Potato." *Ann. Applied Biol.* **14**, pp. 113-131. 1927.

Experiments showed that certain aphids can transmit the virus of the disease from one plant to another; evidence was obtained that some other plant-sucking insects can also probably carry it.

7. THE NUMBERS OF ANIMALS.

Watt, H. Boyd. "Observations on the American Grey Squirrel in Britain." *School Nature Study*, **21**, pp. 1-3. Jan. 1926.

An important summary of the present situation of the introduced Grey Squirrel, with notes on its spread and habits. The author shows that the decrease in Red Squirrels is probably only a coincidence, since they have decreased in many places in the absence of the Grey Squirrel.

Mason, F. A. "Natural History of Grass Wood and its Environs." *Naturalist*, 1927, pp. 205-214.

Only one Red Squirrel was seen in June 1927; formerly it was quite common in this wood.

Fortune, R. "Mammals." *Naturalist*, 1927, p. 298.

Grey Squirrel near Market Weighton, Yorks.

Smith, S. H. "Mammals." *Naturalist*, 1927, p. 21.

Includes a note on the increase and spread of the Grey Squirrel and the decrease of the Red Squirrel in Yorkshire.

Wallis, C. W. K. "Nature Notes in Edgbaston Park." *Proc. Birmingham Nat. Hist. and Phil Soc.* **15**, pp. 117-123. 1926-27.

Red Squirrel was there thirty years ago, but now has been replaced by the Grey Squirrel.

Stelfox, A. W. "The Grey Squirrel spreads to Westmeath." *Irish Nat. Journal*, **1**, p. 275. 1927.

This squirrel was introduced into Ireland (in Co. Longford) a few years ago.

Moffat, C. B. "The Squirrel." *Irish Naturalists' Journal*, **1**, pp. 250-252. 1927.

Red Squirrels became suddenly very scarce in many parts of Ireland between the years 1908 and 1912, and they are only now beginning to regain their former numbers. The Grey Squirrel is not driving out the Red, except in parts of Co. Longford, where it has been introduced.

Moffat, C. B. "The Lesser or Pigmy Shrew." *Irish Naturalists' Journal*, **1**, pp. 66-68. 1926.

Contains notes on the breeding season of shrews, and an account of an epidemic amongst pigmy shrews in Denbighshire, in July 1925.

Smith, S. H. "Annual Report of the Yorkshire Naturalists' Union for 1925; Mammals." *Naturalist*, 1926, p. 12.

Mentions epidemic of a "fungus-like" disease killing hares in East Riding in 1925; also a similar one among rabbits on the Wolds, some years before. Notes the unaccountable decrease of Red Squirrel in Yorkshire, where they are not much shot.

Witherby, H. F. (edited by). "The 1927 Irruption of the Crossbill." *British Birds*, **21**, pp. 90-93, 153-155 and 174-177. 1927.

Anon. "A Crossbill Influx from Europe." *Scottish Nat.* 1927, pp. 126-127, 158-160 and 164.

The last big movement before this one (1927) was in 1909, with smaller groups or individuals in 1911 (p. 126).

Forrest, H. E. "The Crossbill Invasion." *North Western Nat.* **2**, pp. 175-176. 1927.

Turner, S. T. C. "Ornithological Section." *Rept. of the Marlborough College Nat. Hist. Soc.* for 1927, No. 76, p. 19. 1928.

Contains notes on occurrence of crossbills.

Tucker, B. W. (edited by). "Report of the Ornithological Section of the Ashmolean Society and the Oxford Ornithological Society for 1926." *Proc. and Rept. of Ashmolean Nat. Hist. Soc. of Oxfordshire* for 1926, pp. 1-26, 1928. Similar Report for 1927, same journal, pp. 1-36, 1928.

These two reports are chiefly devoted to notes on the numbers and distribution from year to year of birds in Oxfordshire, Berkshire, and Buckinghamshire, together with records of dates of arrival of migrants, and occurrence of rarities. In addition there are, in the Report for 1927, a number of notes of more immediate ecological interest, e.g. the location of starling-roosts, and habits of the birds; the crossbill irruption of 1927; the effects of severe weather in the winter of 1927-28 upon small birds; the Oxford Bird Census Scheme; etc., etc.

Wade, E. M. "Vertebrate Zoology Committee: East Riding." *Naturalist*, 1927, p. 18.

Notes mortality among small birds (especially Tits and Redwings) in Yorkshire in the severe winter of 1925-26.

Doe, G. M. "Plague of Starlings." *Trans. Devon. Ass. for Advancement of Sci., Lit. and Art*, **59**, pp. 223-225. 1927.

An account of damage done to trees by huge flocks of starlings roosting in them during autumn and winter.

Rintoul, L. J. and Baxter, E. V. "On the Decrease of Blackgame in Scotland." *Scottish Nat.* 1927, pp. 5-13, 45-52 and 69-75.

A careful analysis of the fluctuations in numbers of this species, which have been very great during the last hundred and fifty years, not only in Scotland, but also in Holland, Sweden, Norway, and Finland. The causes of the fluctuations are discussed, but no final conclusion is reached by the authors.

Scone. "Wood-Pigeon Diphtheria in Perthshire." *British Birds*, **21**, p. 19. 1927.

Epidemic in Feb. and March 1927. References to some previous epidemics are given.

Thursley-Pelham, D. E. "Some Effects of the Closure of the North Sea to Fishing during the Great War, and of the Resumption of Fishing."

Trans. Norfolk and Norwich Nat. Soc. **12**, pp. 322-335. 1926-27.

A very interesting analysis of the effect of human depredations on the flatfish of the North Sea. During the War, many parts of the North Sea were closed to fishermen, and in consequence the fish increased in numbers, until there were, in 1919, about twice as many plaice, soles, and turbot, as there had been in 1913 and 1914. After the War, the flatfish population began to fall again.

The author also states that haddock are subject to violent fluctuations in numbers, due to natural causes, probably acting on the eggs and larvae.

Robertson, D. "Notes on Soil Nematoda." *Proc. Royal Physical Soc. Edinburgh*, **21**, pp. 83-88. 1926.

A list of species found in various soils, together with an account of two methods of carrying out censuses. The results of sampling by these methods showed that there were from 1.32 to 4.33 billion nematodes per acre of soil (in the top six inches).

Morris, H. M. "The Insect and other Invertebrate Fauna of Arable Land at Rothamsted. Part 2." *Ann. Applied Biol.* **14**, pp. 442-464. 1927.

Primarily a census of the soil animals in a field of clay and flints, over chalk, on which mangolds had been grown since 1876 and which was divided into plots, manured in different ways. Describes methods of taking samples. Also contains long lists of the animals, together with their seasonal occurrence and numbers. The species are given in the case of Collembola, Coleoptera, most Diptera, and Myriapoda; they are mentioned, but not identified, in the case of Spiders, Mites, Hemiptera, Hymenoptera, many Diptera, and Worms. It is shown that manuring with dung increases greatly the number of animals living in the soil, but that artificial manuring does not increase them very much.

Adkin, R. "The Balance in Nature." *Proc. South London Entom. and Nat. Hist. Soc.* 1927, pp. 45-54.

The variations from year to year in the numbers and distribution of certain Lepidoptera are described and discussed.

Walton, C. L. "Notes on the Activities of Humble Bees (*Bombus*) in North Wales." *Ann. Applied Biol.* **14**, pp. 465-469. 1927.

A list of species observed in North Wales (with a few also from Herefordshire and Montgomeryshire) between 1923 and 1926. Contains full notes on each species, as regards flowers visited, seasonal occurrence, and numbers.

Cuthbertson, A. "Note on an Ichneumon (*Stenichneumon trilineatus* Grav.), parasite of the Magpie-Moth (*Abraxas grossulariata*, Steph.)." *Scottish Nat.* 1927, p. 24.

Twenty-five per cent. of the moth larvae bred were parasitised.

Till, A. S. "*Apion Ulicis*." *Rept. of the Marlborough College Nat. Hist. Soc.* for 1927, No. 76, p. 76. 1928.

Fifty per cent. of the pods of gorse, in one area, were found to contain larvae of this weevil.

Britten, H. "Abundance of *Haematopota pluvialis* L. in Cumberland and Westmorland." *North Western Nat.* **1**, p. 147. 1926.

Unusual abundance of this blood-sucking fly in June and July.

Ritchie, J. "An account of the destruction of Methil Dock gates by marine organisms." *Scottish Nat.* 1927, pp. 37-44.

The damage was caused by two Crustacea, the amphipod *Chelura terebans*, and the isopod *Limnoria lignorum*.

Ritchie, J. "A remarkable Whale Invasion." *Scottish Nat.* 1927, pp. 161-163.

A school of False Killers (*Pseudorca crassidens*) visited the Dornoch Firth in October 1927, and some of them ran aground there. This whale is very rare, and had hardly been seen anywhere for 80 years (a few appeared off Western Europe in 1861 and 1862, and it was also seen in Tasmania). Examination of these whales showed that they feed mainly on large cuttle-fish.

8. DISPERSAL AND BIRD-MIGRATION.

Boase, H. "Local Migration in Autumn in South-West Forfarshire." *British Birds*, **21**, pp. 31-37. 1927.

An interesting account of the way in which autumn migration starts among certain small birds (e.g. tits and warblers). It appears to start as a slow "drift," the birds forming small parties, often of mixed species.

Triffitt, M. J. "Observations on the Morphology and Bionomics of *Rhabditis coarctata* Leuck. occurring on Dung Beetles." *Journ. Helminthology*, **5**, pp. 33-46. 1927.

Rhabditis coarctata is a roundworm, which was found living in sheep dung. It was found, further, to have the habit of attaching itself on to various dung beetles (species of *Aphodius*, *Cercyon*, and *Oxytelus*) and encysting, and in this way becoming transported to new patches of dung, where it then drops off and completes its development as a free-living worm. A short list of dung beetles from sheep dung is given incidentally.

9. EFFECTS OF GRAZING ON VEGETATION.

Fenton, E. W. "The Influence of Grazing on Vegetation." *Trans. and Proc. Torquay Nat. Hist. Soc.* **4**, pp. 315-323. 1926.

Discusses the effect of different domestic animals on the plant associations, giving lists of species under various grazing conditions. One case is described, where grassland reverted to *Calluna* heath after being protected for three years from sheep and cattle grazing.

FURTHER CHANGES IN THE SALT MARSH AND SAND DUNES OF HOLME-NEXT-THE-SEA

By T. R. PEACE.

(With two Figures in the Text.)

THE observations in these notes form a continuation of the work carried out by parties of students in 1913-14 and again in 1920, and published (1), (2) in this JOURNAL. References to special pages in these papers are made below. The work for this paper was carried out on two visits to the marsh in March 1927 and March 1928.

For purposes of survey in 1913 a base line seven furlongs (1408 m.) in length was staked out in lengths of one furlong. Four of the old posts were found in March 1928, and the positions of the others could thus easily be determined. The map (Fig. 1), which gives a rough outline of the marsh and dunes as they were in March 1928, was prepared from a rough survey using this base line and posts. This map should be compared with Figs. 1 and 2 in (2). It serves to show the main alterations in the marsh. These will be dealt with under convenient headings, which correspond to a certain extent with those in (2).

THE OUTER DUNES.

The new dune in V-VI, N. and VI-VII, N. is now completely consolidated on to the older range, except in the west end of VI-VII, N. where it is still separated from the older dune by a lagoon, which is filled by the higher spring tides. Ephemerals are still rare on this new dune.

Bellis perennis has now appeared on the older dune in VI-VII, N. The western end of the dune is now covered with huts and bungalows; and weeds of cultivation and cultivated plants have spread from the flower beds which have been made near some of these. As an example of the first there is a small area near one bed where *Capsella bursa-pastoris* is very common. And as an example of the second there is a clump of *Iris germanica* established at one point at the back of the dunes.

Both the new dune and the older dune are being rapidly eroded, the former in VI-VII, N. and V-VI, N. and the latter in IV-V, N. and III-IV, N. where it is not protected by the new dune. In the case of the older dune erosion has passed the old crest, and the bank now consists of a gentle slope down to the marsh on the landward, and a steep sand cliff $1\frac{1}{2}$ -2 metres high down to the shingle beach on the seaward side. *Ammophila* is making no attempt to colonise the eroded face; erosion is probably too continuous. If this erosion continues the marsh will ultimately become open to the sea.

THE SOUTHERN DUNES.

Since 1920 the sandy cliff at Gore Point has receded a further 10 metres; so that now the point 0 on the base line is at the outer margin of the narrow shingle bank which flanks the dunes at this point. Serious erosion has taken place south of point I where the stream from the marsh now impinges on the dunes. It is proposed by those in charge of the dunes to remedy this by removing the end of the shingle bank, and placing it in the stream where it touches the dunes. This and other erosion east of Gore Point has caused anxiety lest the drained grazing marshes, which are protected by the dunes, should

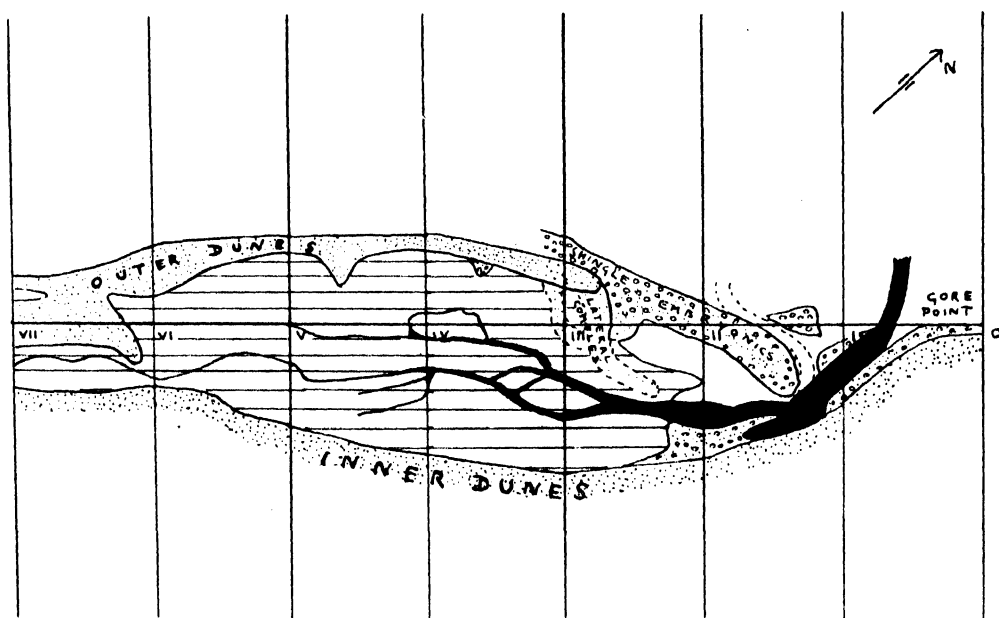


FIG. 1. Sketch-map of the marsh in 1928. Horizontal lines indicate the area covered by marsh vegetation. The distances from 0-I, I-II, etc. are 220 yds. (200 m.).

again be flooded as they were about 50 years ago. The breach in the bank on this occasion was 300 metres east of Gore Point. I have been informed from a reliable source that while the grazing marsh was still flooded by spring tides *Salicornia* appeared in the place of the grasses, which were all killed by the salt. After the bank was repaired a white clover was the primary colonist on the marsh. It appeared at first in isolated patches, and finally formed a closed sward. It formed a very rich grazing on the marsh for three or four years, when it was replaced by grasses. This should be compared with Ganong's account of deliberate "tiding" (3). In his case *Salicornia*, *Suaeda maritima* and *Atriplex patula* were the chief primary colonists. But the first non-halophytes to appear after the banks had been repaired were the various grasses typical of the diked marshes. It should also be compared with Massart's

observations on the Yser (4). In this case *Aster tripolium* and *Atriplex* spp. were the primary colonists; and when the salt was washed out a mixed weed flora colonised the mud.

In March 1927 three sods bearing *Calluna* and *Erica* were transplanted from a heath near Dersingham to positions behind the dunes in 0-I, S. Only one of these has survived. This bears a healthy plant of *Erica cinerea*, which, however, shows very evident signs of rabbit attack. It is in a "dune hollow" (1, p. 79), and therefore in a position with a fairly good water supply. It appears probable that *Erica* and *Calluna* would become established here if they could arrive in sufficient numbers to resist rabbit attack. But the nearest habitats of these plants and of *Pteridium* are too distant for them to reach the dunes at all easily.

THE SHINGLE BANK AND THE MOUTH OF THE STREAM.

The shingle bank in I-II, N. and II-III, N. has not moved to any extent since 1920. It has now (1928) quite fused on to the dune. The mouth of the stream however has shifted considerably. It now impinges directly on the dunes in I-II, S. and passes out to sea in 0-I, N. In 1927 it still flowed out to sea in II-III, N. as shown by the dotted lines in the map (Fig. 1). Several new shingle "patches" have arisen in connection with the new entrance. But these are but little raised above the surrounding sand and show no signs of permanence.

The embryonic dunes on the shingle bank are now much closer, and extend right along the bank to the dune. On the crest in I-II, N. they almost form a closed system. In this part *Agropyrum junceum* and *Ammophila* are co-dominant, *Arenaria peploides* is frequent, and *Elymus arenarius* occurs in a few places.

THE LATERALS.

The lateral in VI-VII, N. has not altered. There is a colony of *Plantago coronopus* on the edge nearest the marsh. The lateral in IV-V, N. is partly covered by a refuse heap. These are becoming regrettably common round the margins of the marsh. A number of "weeds" have appeared in and around this heap. These include *Lamium album*, *Malva sylvestris*, etc.

The complex in II-III, N. has now the appearance of two laterals separated by a narrow bay, the western one being shorter and lower. Both are intersected by channels and pools. The western one consists of sandy hummocks with *Agropyrum* and *Obione*. The *Suaeda fruticosa* bushes are rather unhealthy. This is also the case on the laterals in III-IV, N. and IV-V, N. At the ends of these laterals and in the lower-lying parts of the western lateral of the complex this is probably due to the deposition of mud (1, p. 74). But on the higher parts the bushes probably find the soil too stable (5, p. 267), the amount of drift and silt deposited in these positions being insufficient for the healthy growth of the plant. In the hollows in this lateral *Cochlearia* is particularly frequent.

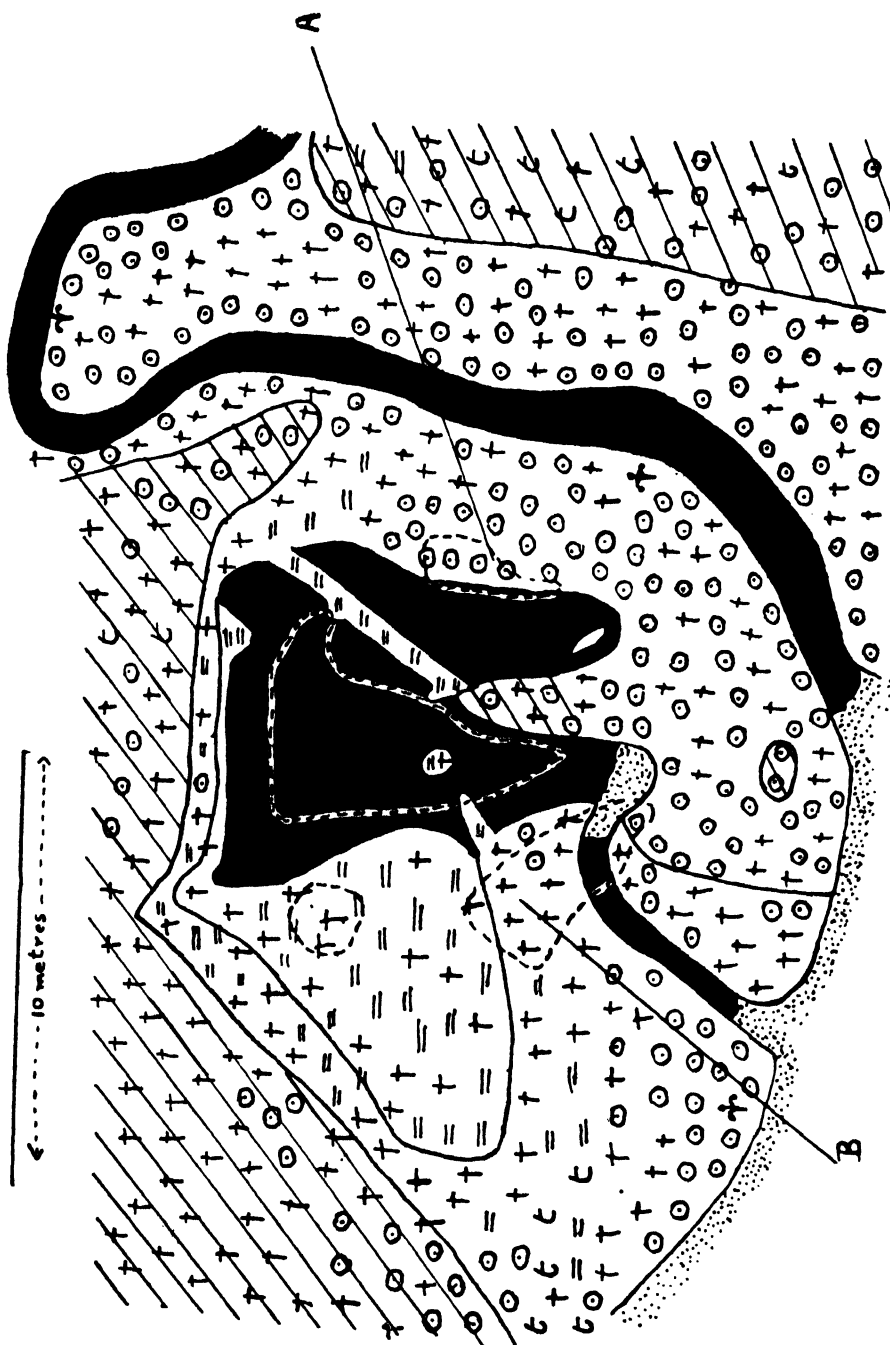


FIG. 2. Vegetation Chart of an area containing a pan which was artificially drained in 1913. This map was made in 1927.
Black area indicate exposed mud. Dotted area indicates exposed sand.

// *Statice limonium*. † *Glyceria maritima*. ○ *Obione portulacoides*. = *Aster tripolium*. t *Triglochin maritimum*. ♦ *Suaeda fruticosa*.

The eastern and longer lateral is rather higher. *Obione* and *Agropyrum* occupy most of the hummocks, but *Suaeda fruticosa* is spreading rapidly, and healthy seedlings of this plant are very abundant. Deposition of sand on this lateral takes place at a moderate rate, and this instability probably favours *Suaeda*.

THE SALT MARSH.

No appreciable alteration has taken place in the western and central parts of the marsh. At the eastern end a small new marsh is spreading eastwards and northwards from the new lateral across the mud flat in II-III, N. This mud flat has an open vegetation of *Salicornia* with a few plants of *Suaeda maritima*. The new marsh mostly consists of *Glyceria* but *Salicornia* occurs in the incipient pans and channels. *Aster* is fairly frequent, and a few plants of *Statice limonium* were found in the older parts near the lateral.

The western edge of the shingle bank, which replaced the original *Salicornia* flats (2, p. 235) south of the stream, has receded since March 1927. *Glyceria* has colonised the sandy mud which was thus uncovered.

THE PANS.

The primary pan which was drained in 1913 and mapped in 1914 and in 1920 (2, Figs. 3 and 4) was again mapped (Fig. 2). The artificial exit made in 1913 had been partially blocked in 1920. It is now even more blocked up. About four days after the last spring tide had covered the marsh all the bare mud and all the area covered by *Aster* was immersed, the water thus covering an area almost as large as the original pan. The colonisation by *Aster* of parts of the old pan which in 1920 were occupied mostly by *Glyceria* is the most interesting change. *Aster* appears to be able to withstand more prolonged immersion than *Glyceria*. This is now the most extensive patch of *Aster* in the marsh. The old pan margin has almost entirely disappeared. The exit is still being closed by *Glyceria*, and it will be interesting to observe the reaction of *Aster* to yet more prolonged immersion. *Obione* has encroached on the area occupied by the old pan at the point A on the figure. *Glyceria* (at the point B) has built up quite a high hummock in what was actually part of the old pan. Extension of this hummock southwards appears to be the main factor concerned in the blocking of the exit.

Salicornia (by seed) and *Glyceria* (by growth over the margins) are the chief colonists of naturally drying or drained pans in all parts of the marsh. A large pan in the *Armeria-Statice* zone near point V, drained in 1921, was colonised in this manner; as also were pans in the *Armeria* zone which were drying up owing to infrequent immersion. A pan in the *Glyceria* zone in II-III, S. drained in March 1927 had in the summer of 1927 a few *Salicornia* plants in the higher parts, and *Glyceria* has now reached the bottom of the pan in a few places (March 1928). *Obione* appears occasionally to act as a weak colonist, crawling over the margins in the same way as *Glyceria*. This was

seen in the pan drained in 1921 and also in drying-up pans in the *Armeria* zone. In all cases the *Obione* was rooted in the mud at the bottom of the pan, but had not extended much.

The writer is greatly indebted to Mr Wadham, without whose encouragement his investigation of the marsh would never have been attempted, and to his sister for help with the survey and other observations made on the second visit.

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- (1) **Marsh, A. S.** "The Maritime Ecology of Holme-next-the-Sea, Norfolk." This JOURNAL, **3**, 1915.
- (2) **Wadham, S. M.** "Changes in the Salt Marsh and Sand Dunes of Holme-next-the-Sea." This JOURNAL, **8**, 1920.
- (3) **Ganong, W. F.** "The Vegetation of the Bay of Fundy Diked and Salt Marshes; an Ecological Study." *Botanical Gazette*, 1903.
- (4) **Massart, J.** "La Biologie des Inondations de l'Yser, et la Flore de Ruines de Nieuport." Bruxelles, 1922. Notice in this JOURNAL, 1922.
- (5) **Oliver, F. W.** and **Salisbury, E. J.** "Vegetation and Mobile Ground as illustrated by *Suaeda fruticosa*." This JOURNAL, **1**, 1913.

NOTE ON THE ECOLOGY OF MYCORRHIZA

I AM indebted to the reviewer of my book *Mycorrhiza* (Rayner, 1927) in this JOURNAL (1928) for enabling me to realise that the omission from it of a section dealing with the phenomenon from a strictly synecological standpoint has left my views open to misconception. I am grateful for the opportunity now afforded to clear myself from any ambiguity in the matter.

While agreeing that older views respecting the significance of mycorrhiza to the participants were frequently dictated by too teleological a view, the critical paragraphs dealing with what is regarded as a misuse of the term *symbiosis* in the monograph under discussion, apart from opinions expressed in previous papers, should have made my own position unmistakably clear.

In general, I regard mycorrhiza as an ecological phenomenon resulting directly from the inevitable competition in soil between roots of vascular plants and the mycelium of numerous soil fungi. Originating in the facultative parasitism or quasi-parasitism of the fungi concerned, possibly favoured by the presence of exudates in the neighbourhood of roots, the relation is inhibited or established and often rendered relatively stable, by the interaction of those properties—common alike to plant and animal cells—upon which depend the qualities known as susceptibility, resistance and immunity. Regarding the incidence of fungus attack simply as one of a number of biologic soil factors, it is clear that, like others, it is subject to great variation in relation to differences in external conditions, viz. temperature, moisture, and the soil content of humus and nutritive salts, all these operating directly and also perhaps indirectly by affecting the capacity for attack on the one hand and resistance on the other.

Casual and intermittent in many plants, in others mycorrhiza has become a regular feature in the life-history, so acquiring a relative stability as an effective factor in the constitution of the vascular hosts that appears to me to remove it from the ecological category of biologic soil factors in general.

In respect to the relationship between vascular plant and fungus in those mycorrhiza plants in which fungus infection is relatively inconstant and irregular and for which no experimental data are at present available, I hold and have expressed precisely the views now stated by my reviewer, viz. "there must be every degree of transition between the extreme cases where a parasite attacks (and kills) a 'host,' and a delicately adjusted equilibrium between two organisms which continue to live in intimate connection because the forces tending to maintain each in its relation to the other are accurately balanced." At present these must be regarded biologically as interesting cases of compromise—to some extent casual and determined largely by local soil conditions—fluctuating between almost complete resistance to fungus invasion and a remarkable toleration of the same. That there is a "give and take" of nutritive material in practically all cases hardly admits of doubt, but it is probably irregular and intermittent. In the absence of information based on the behaviour of individuals with and without mycorrhiza, attempts to estimate the permanent advantage or disadvantage to one or other of the symbionts are certainly premature.

In respect to certain groups—orchids, heaths and to a lesser extent forest trees—the case is entirely different, and it was to these experimentally studied examples only that the discussion criticised by my reviewer related.

In particular, the two first-named groups, long known as obligate mycorrhiza formers under natural conditions, constitute a special case. In both, critical experimental study has placed certain facts beyond doubt; in both, normal development of the seedling is bound up

with the presence and activities of mycorrhizal fungi specific to the species, and, in members of *Ericaceae*, this obligate relation is accompanied by a distribution of mycelium throughout the tissues so extensive and so constant that it is difficult to conceive of the individual plant as other than a single entity of double constitution.

The constant association of ericaceous species with edaphic conditions of a characteristic type in nature and the impatience of some of the species under cultivation to changes in these conditions is significant in this connection, while it has been placed beyond doubt that in these plants the development of the root fungus to form typical mycorrhiza is directly controlled by the character of the rooting medium, reaching a maximum in the humus soils with which they are typically associated.

The case of forest trees is somewhat different, but here also we are dealing with an ecological group well defined in relation with edaphic conditions and here also experiment has revealed well-marked specialisation in some of the root fungi, a certain degree of specificity in relation to particular hosts on the part of some of them, and a direct correlation between soil conditions and mycorrhiza development.

In all three groups there is a regular and demonstrable periodic exchange of nutritive material. In orchids, and still more in heaths, the physiological activities of the symbionts are inextricably bound up at certain stages of development--the fact that this phenomenon can be modified artificially under experimental conditions in orchids and possibly also in heaths does not affect the argument. That the physiological relation is delicately balanced is clear. In nature relatively stable in equilibrium, it can readily be disturbed under the "pure culture" conditions of laboratory technique.

Intensive study of these groups has been directed to discover the true nature of the physiological relation between the symbionts. In cases of mycorrhiza for which these relations are inferred only from observations of the structural features, attempts to express them in terms of mutual exchange are certainly premature and often misleading. In those supported by experimentally proven facts, they are (surely) legitimate and desirable.

It is true that "in ecology, where we deal with animal and plant communities which consist of many different species, each eaten by others from inside and outside, each living in amity with some of its neighbours, in competition with others" (Haldane, 1927), it is unwise to dogmatise and usually futile to attempt to express most of the shifting relationships in terms of mutual benefit or the reverse. It is equally true that this confusion of interests supplies the raw material from which the biologist selects individual problems well suited to the methods of exact experimental research and capable of yielding results often of marked theoretical interest, and not infrequently of far-reaching practical importance.

M. C. RAYNER.

HALDANE, J. B. S. (1927). *Possible Worlds*, p. 141.

Journal of Ecology (1928), **16**, No. 1, p. 169.

RAYNER, M. C. (1927). *Mycorrhiza*. Wheldon and Wesley, London.

[We are glad to publish Dr Rayner's able general statement of the ecological relation between fungus and higher plant, which aptly supplements her book. It only remains to add that the criticism referred to of "the polemic on this subject" as "partly sustained by too teleological a view" clearly has no point against Dr Rayner's own writings, but was directed against the general course of controversy (often quite unnecessary and misleading) on the nature of mycorrhiza during the past quarter of a century. ED. JOURNAL OF ECOLOGY.]

BRITISH EMPIRE VEGETATION ABSTRACTS:

TITLES AND ABSTRACTS OF PUBLICATIONS ON THE VEGETATION AND ECOLOGY OF THE OVERSEAS EMPIRE AND ON RELATED TOPICS

PREFATORY NOTE

THIS Supplement to *The Journal of Ecology* contains the first instalment of the Titles and Abstracts of publications on the Vegetation and Ecology of the Overseas Empire and on related topics to be published under the scheme of the British Empire Vegetation Committee described in *Journ. Ecol.* **15**, 2, p. 376 (August, 1927). It has not been found practicable to prepare a complete set of abstracts for 1927 for the present issue, so that the scheme has been made to begin with publications bearing the date 1926, to which year all the abstracts in this Supplement relate.

The Titles and Abstracts will be arranged under the following Geographical Headings: (1) Canada, (2) South Africa, (3) Australia, (4) New Zealand, (5) Pacific Islands, (6) Malaya and East Indies, (7) India, Burma and Ceylon, (8) Tropical and North Africa, (9) Central and South America. Of these (1), (2), (3), (4), (5) and (7) are represented in the present issue.

They will be numbered consecutively throughout, and following each citation the numbers in brackets refer to the Geographical Section and the number of the paper cited *in* that section. The Supplements will be paged separately from the body of the *Journal*, thus: "Suppt 1."

Each issue of the Supplement will be included in the issue of the *Journal* with which it appears and the Supplements will be included in the subscription price of the *Journal*. The Supplements will also be supplied apart from the *Journal* at a subscription price of 5 shillings a year payable in advance on application to the Hon. Secretary of the British Empire Vegetation Committee (Dr T. F. Chipp, 199 Kew Road, Kew, England), from whom full particulars of the scheme may be obtained. *Individual* Supplements will not be sold separately.

(1) CANADA (COLLABORATOR, R. D'O. GOOD)

1. **Lewis, F. J. and Dowding, E. S.** "The Vegetation and Retrogressive Changes of Peat Areas ('Muskegs') in Central Alberta."¹ *Journal of Ecology*, **14**, pp. 317-341. 1926. (1. 1.)

The term "muskeg" as used in Canada is practically synonymous with peat-area but *Sphagnum* is usually a more pronounced feature in the vegetation than it is in Britain and the peat generally bears trees. *Calluna*, as the dominant ericaceous plant, is replaced by *Ledum*. Muskegs are chiefly found in the parkland and northern coniferous forest and are absent from the prairie. Several typical kinds of muskegs in the vicinity of Edmonton

¹ The authors desire this paper to be considered as the first of a series on "The Vegetation of Alberta," though these words do not appear in the title as printed in *The Journal of Ecology*.

are described. One is wholly dominated by *Sphagnum* and in others this has been replaced by *Ledum* which is still dominant but obviously dying out. Plenty of peat indicates the former abundance of *Sphagnum* and there is a border of *Carex* showing signs of invasion by *Salix*. A more detailed account is given of a particular muskeg known as Stony Plain Muskeg. This is partly true muskeg and partly open lake. In the former *Ledum* is dominant but beginning to disappear and there is a considerable thickness of peat underlain by a blue clay containing seeds of aquatic plants and shells of Gastropods. The lake also overlies peat but the water is filled nearly to the surface with a calcareous algal deposit.

It is concluded that the muskegs began as shallow lakes left in basins of glacial deposits when the ice retreated: that these were first colonised by aquatic plants followed by *Sphagnum* until sufficient peat was formed for the invasion of trees and that after this desiccation set in, *Ledum* replacing the *Sphagnum* and being in turn replaced by other plants. Sometimes calcareous and magnesium springs burst through the muskeg arresting the succession and resulting in a thick subaqueous deposit. At the present time the muskegs of the parklands are all small and show much retrogression and it is not until the forests are reached that large areas of *Sphagnum* occur.

It would seem that the chief cause of retrogression is increasing climatic desiccation. The present annual rainfall of from 12-22 inches and a growing season of four months are conditions hardly suitable for the production of large quantities of peat.

Forest fires are also suggested as a cause of drying-out but the authors do not attach much importance to this and produce evidence indicating that a muskeg, at least in its earlier stages, can regain its original condition after being burnt over.

The paper concludes with an account of the investigation of the growth rings in some of the trees growing in muskegs. It would appear that there have been, in the last century, two maximum periods of rainfall (about 1835 and 1915) and a period of drought (about 1885). It is also found that the rate of tree growth is roughly inversely proportional to that of *Sphagnum* and that trees in muskegs which are drying-out are growing about four times as fast as those in muskegs which are still in full growth.

2. Bisby, G. R., Connors, I. L. and Bailey, D. L. "The Parasitic Fungi found in Manitoba." *Bull. Dept. Agric. Can.* 71. 1926. (1. 2.)

3. Krebs, C. "The Lotus in Northern Ontario." *American Botanist*, 32. April, 1926. (1. 3.)

4. Campbell, D. H. *Outline of Plant Geography*. London: Macmillan and Co. 1926. Pp. ix + 392, 52 plates, 101 figs. (1. 4.)

The book is arranged geographically. Chapter iv gives a general illustrated account of the vegetation of the Atlantic and Central United States and Canada. Chapter v gives a similar account of the Rocky Mountains and Pacific Slope.

5. Moss, E. H. "Parasitism in the Genus *Comandra*." *New Phytologist*, 25, pp. 264-276. 1926. (1. 5.)

A general account is given of the semi-parasitic habit and the host-plants of the genus and special reference is made to the species *C. livida* Richards and *C. richardsoniana* Fernald. The haustorium is very like that described for *Santalum*. The method of penetration of the haustorium is described, and the occurrence of self-parasitism in the genus is noted. Attention is also drawn to numerous variegated and dwarfed individuals of *C. livida*, whose leaves exhibit features characteristic of mosaic disease. There are 9 text-figures and a short bibliography.

6. **Marie-Victorin, Frère.** "Notes pour servir à l'Histoire de nos Connaissances sur les Abietacées du Quebec." *Proc. and Trans. Roy. Soc. Can. Ser. III*, **20**, pp. 437-460. 1926. (1. 6.).

This paper consists of a series of notes, arranged systematically, on the records and work of the earlier collectors and explorers in Quebec. There is a bibliography, one text-figure and plates of the title-pages of three early botanical works.

7. **Marie-Victorin, Frère.** "Études sur les Composées du Quebec." *Proc. and Trans. Roy. Soc. Can. Ser. III*, **20**, pp. 461-482. 1926. (1. 7.)

Miscellaneous notes on the genera *Solidago*, *Aster*, *Eupatorium*, *Bidens*, *Erigeron*, *Antennaria*, *Hieracium*. Three new hybrids are described—*Solidago altissima* × *canadensis*, *Aster cordifolius* × *paniculatus*, *Aster novae-angliae* × *paniculatus*; one new variety, *Erigeron lonchophyllus* Hook. var. *laurentianus* Vict. and one new form, *Eupatorium urticaefolium* Reichard f. *verticillatum* Vict. Distribution maps of *Erigeron lonchophyllus* and its variety and of three groups of species in *Antennaria* (*A. carpathica*, *A. alpina*, *A. plantaginifolia*) are given in the text. There are plates of *Aster anticostensis* Fernald and of its habitat; of *Erigeron lonchophyllus* and variety and of the new *Aster* hybrids.

8. **Perry, Fred.** "Mosses in British Columbia—their Importance under Local Conditions." *Can. Field Nat.* **40**, pp. 81-83. 1926. (1. 8.)

A list of the commoner species of mosses, with notes on their habitat.

9. **Ball, C. R.** "Canadian Willows of Sections Pentandrae, Nigrae, Albae and Longifoliae." *Can. Field Nat.* **40**, pp. 145-153, 171-177. 1926. (1. 9.)

A complete revision with full notes and clavis of the eleven native species, one introduced species and seven varieties in these groups. One new combination is made, *Salix interior pedicellata* (Anderson) Ball.

10. **Dodge, C. W.** "Lichens of the Gaspé Peninsula, Quebec." *Rhodora*, **28**, pp. 157 et seq. 1926. (1. 10.)

A short chronological introduction and a list of all species, varieties, etc., with localities and collector's numbers. Two new combinations are made, *Lecidea (Biatora) peliaspis* (Tuck.) and *Batidea leucampyx* (Tuck.).

(2) SOUTH AFRICA (COLLABORATOR, A. W. EXELL)

11. **Phillips, J. F. V.** "*Virgilia capensis* Lamk. (Keurboom): A Contribution to its Ecology and Sylviculture." *S. Afr. Journ. Sci.* **23**, pp. 435-453. 1926. (2. 1.)

Virgilia is a monotypic genus of Papilionaceae restricted in distribution to the coastal belt of the south-west of South Africa.

It is a light-demanding tree which is prominent in the seral stages of the forest succession, gradually replacing the *Macchia* and eventually being ousted by trees of larger growth. It is more abundant, however, as a subsera where forest or *Macchia* have been removed by fire or other agency, when it may form a sub-climax for many years.

The biology of the flowers and fruits and the dispersal of the seeds are discussed. The latter may remain dormant for many years and indeed only start growth after stimulation by damage to the testa, etc.

The question of the restricted distribution is discussed and it is concluded that it is an old but virile species that has been unable to spread beyond its present narrow limits owing to its inefficient means of seed dispersal, habitat requirements such as soil-moisture and non-occurrence of severe frost, and to the possible absence inland of the particular strain of *Pseudomonas radicicola* (Beijk.) Moore necessary for the development of the nodules.

The tree is of value in forestry as a fast-growing cover to other species and the timber is suitable for spars, yokes, etc.

- 12. Phillips, J. F. V.** "The Propagation of 'Stinkwood' (*Ocotea bullata* E. Mey.) by Vegetative Means." *S. Afr. Journ. Sci.* **23**, pp. 418-434. 1926. (2. 2.)

Ocotea bullata E. Mey., the "Stinkwood" or "Laurel," is a valuable forest tree that is usually propagated by seed, but as the germination capacity is low (only 0.1 per cent. of the fruits contain fertile seed), the problem of its regeneration is of practical importance.

Many methods of vegetative propagation were attempted, cuttings treated in many ways, propagation by buds or leaves, root cuttings, layers and truncheons; but in no case was there any appreciable success of practical value.

- 13. Phillips, J. F. V.** "General Biology of the Flowers, Fruits and Young Regeneration of the more important Species of the Knysna Forests." *S. Afr. Journ. Sci.* **23**, pp. 366-417. 1926. (2. 3.)

Information concerning the biology of the flowers, fruits and young regeneration of 63 species of trees and shrubs of the Knysna forests is given and summarised in tabular form. The seasons of flowering and fruiting, pollination phenomena, nature, efficiency, dispersal and germination of the seeds, and the establishment and fate of young regeneration are investigated.

A feature of interest is the influence of proximity to the ocean on earlier date of flowering and fruiting of all species.

- 14. Henrici, Marguerite.** "Growth of Veld Plants under arid Conditions of Bechuanaland." *S. Afr. Journ. Sci.* **23**, pp. 325-339, 4 figs. 1926. (2. 4.)

Growth measurements were made of plants in their natural habitats near Vryburg in Bechuanaland, a region with a rainless winter, where the soil moisture often falls to 2 per cent. and the atmospheric relative humidity to 20 per cent. The plants were exposed to full insolation and the measurements were made with a Pfeffer auxanometer.

The most important factor influencing the growth of grass haulms is the soil moisture, atmospheric humidity playing a relatively small part, and insolation none at all, because always excessive.

Contrary to conceptions of European literature prior to 1918, light does not necessarily prevent growth, for the Bechuanaland grasses grow from three to ten times as fast by day and growth often stops altogether at night. A few plants examined, however, showed an exclusively night growth.

Maximal increases of grass haulms of 0.02 to 0.1 mm. per minute occurred under full insolation.

- 15. Sim, T. R.** "Some Effects of Man's Influence on the South African Flora." *S. Afr. Journ. Sci.* **23**, pp. 492-507. 1926. (2. 5.)

This is a general statement of the problems that arise in connection with the influence of man on the flora of the country. In South Africa this influence is already far-reaching and the statement occurs that "in no locality can the flora be regarded as natural." Both intentional and accidental introductions are discussed.

- 16. Phillips, E. P.** "The Genera of South African Flowering Plants." *Bot. Survey of S. Afr. Memoir No. 10.* Pp. 2-702. Cape Town: Govt. Printer. 1926. Price £1. (2. 6.)

This is a systematic work comprising descriptions of the genera of the Angiosperms and Gymnosperms of the Union of South Africa, with keys to the families and to the genera in each family. Engler's System is followed and a synopsis of the tribes is given in addition to the generic keys. The genera are arranged and numbered according to Dalla Torre and Harms' *Genera Siphonogamarum* and the index refers to the generic numbers in this work.

Short notes on the distribution of each genus are given but these are very much generalised and are without reference to habitat.

Rearrangements and recent revisions are included, notably the Restionaceae (by N. S. Pillans) and the genera associated with *Mesembrianthemum* (by N. E. Brown).

Some introduced plants are included: the limits to be set here must always be arbitrary, but it is difficult to see the reason for the inclusion of such genera as *Hakea* or *Vitis* and not of *Pinus*.

- 17. Report of the Forest Department, Union of South Africa, for year ended March 1926.** Pp. 1-32. Pretoria. (2. 7.)

While as a whole this scarcely deals with vegetation there are some points worthy of note. In a country so largely treeless as South Africa, forestry is of great practical importance.

During the last year 487 acres of drift sand were reclaimed by the planting of Marram followed by the sowing of seeds of *Acacia cyclops* A. Cunn., *A. saligna* Wendl. and *Myrica cordifolia* L. The last was the most successful, as the wattles, in the absence of shelter, were liable to be scorched in summer.

Research work has been carried out on various lines, that on the native forests being on a definitely ecological basis and promising to give results of practical importance.

Aeroplane dusting was employed for the first time in South Africa, the insecticide calcium arsenate being used. The method proved successful but is at present impracticable owing to the expense.

The urgent necessity of further work is emphasised by comparison of the figures for imported timber, fourteen million cubic feet, with the total amount from government forests and plantations, two million.

- 18. Hubbard, C. S.** "A Review of the Species of *Populus* introduced into South Africa." *S. Afr. Journ. Sci.* **23**, pp. 340-365, Plates I-II. 1926. (2. 8.)

Poplars have been cultivated in South Africa for a considerable time but not on any large scale. As a valuable soft wood it is certainly desirable that they should be grown in larger quantity.

Fourteen species are grown in South Africa. The general characters of these are given together with notes on their silviculture and rates of growth where these have been studied.

P. canescens Sm. is much the commonest species. An apparently endemic variety which is almost or quite evergreen is here described as var. *Rossii*. It occurs on the high veld. The possibility that this may have arisen as a climatic adaptation of the normal is considered, but in the Eastern Cape Province, notably at Dordrecht, both forms are growing in close proximity and still maintain their distinctive characters.

P. nigra Linn. var. *italica* Du Roi and *P. deltoides* Marshall var. *missouriensis* Henry are cultivated successfully in the eastern regions. The well-known hybrid *P. serotina* Hartig, was an early introduction. It is of rapid growth and is very frost-resistant. Although it is

rather more exacting in its soil requirements than *P. canescens* it can successfully replace in some situations.

The remaining species are at present in the experimental stage. Poplar wood is largely used for the manufacture of matches.

19. Kotze, J. J. "*Pinus patula* Schl. and Cham., its Introduction into and Growth in South Africa." *S. Afr. Journ. Sci.* **23**, pp. 455-466, Plates III-IV. 1926. (2. 9.)

Pinus patula Schlecht. and Cham. is a native of the Sierra Madre in Mexico, where it occurs at altitudes of 6000-8000 ft. on moist mountains with a rainfall of 30-60 in. In its native locality it forms dense pure stands.

The first plants were sown in South Africa in 1907 and further supplies of seed have been received since. Germination is rapid and good and the seedlings can be planted out after about nine months. The tree thrives best on the mountain slopes of the eastern part of the country. It is able to withstand frost and moderate amounts of snow. It does not flourish in the winter rain regions nor in the Orange Free State, where it cannot withstand the drought.

20. King, N. L. "*Pinus insignis* Doug. (*P. radiata* D. Don) in South Africa." *Journ. Dept. Agric. (S. Afr.)*, 1925. Pp. 71-86, Figs. 1-8 and pp. 220-232. Reprinted as *Forest Dept. Bull. No. 15*. Pp. 1-30, Figs. 1-8. (2. 10.)

This tree is one of the most important in South Africa: it is of rapid growth and gives a yield of saleable timber in a short time.

It is a native of a limited area in California and of the Islands Guadalupe, Santa Rosa and Santa Cruz. The date of its first introduction to South Africa is rather doubtful but it was in cultivation by 1883. The first extensive plantings were carried out in 1884.

A description of the tree is given with notes on the silviculture and management of plantations. Notes and tables of the rates of growth and yield are also given.

The tree needs a rainfall of at least 25 in. and does best in the coastal belt where the rainfall is in winter. If planted inland it should be confined to the cool sides of mountains, high up if the soil is suitable, where mists occur. On the whole the tree is a failure in the Orange Free State and in the Transvaal; while in Natal it should be confined to the mist belt or the Drakensberg area. It dislikes lime and does not do well on badly-drained soils.

Propagation is carried on by seed, and natural regeneration occurs freely under forest conditions, although it does not spread into the native vegetation in a manner similar to *P. pinaster* Soland. The rotation for plantations is from twenty to forty years.

Notes are appended on some of the diseases and dangers to which the trees are exposed.

The timber compares favourably with Baltic deal, the chief drawbacks being a tendency to rough up on planing owing to the numerous knots. Under suitable conditions the financial returns are quite adequate.

The name *Pinus insignis* Doug. has been used throughout for the earlier *P. radiata* D. Don on the score that the former is the more prevalent. There can be no justification for such a practice, which can only retard the attainment of a stable nomenclature.

21. Lonstein, I. "Rapid Colorimetric Determination of Phosphorus in Soils and Vegetation." *S. Afr. Journ. Sci.* **23**, pp. 188-195. 1926. (2. 11.)

The ceruleo-molybdate micro-method used is shown to be accurate for the determination of total and available P_2O_5 in soils and in plant products. There is great economy in time,

and the apparatus is simple enough to be within the scope of a field laboratory. Full details of the technique are given.

- 22. van Zyl, J. P.** "Phosphorus Deficiency in South African Soils and Vegetation." *S. Afr. Journ. Sci.* **23**, pp. 244-252. 1926. (2. 12.)

A number of analyses are given to emphasise the fact that both the soils and crops of South Africa are deficient in phosphorus, when compared with those of other countries. To this deficiency are attributed the cattle diseases "lamsiekte" and "styfsiekte." The unstinted use of phosphatic fertilisers and the development of all the natural phosphatic resources are imperative.

- 23. McClean, A. P. D.** "The History, Phylogeny and Taxonomy of the Genus *Achneria* Munro." *S. Afr. Journ. Sci.* **23**, pp. 273-282. 1926 (2. 13.)

The relationships of the five genera *Eriachne* R. Br., *Achneria* Munro non Beauv., *Pentaschistis* Stapf, *Pentameris* Beauv. and *Danthonia* DC. are considered and the probable lines of ascent from *Danthonia* are indicated. The conclusion is reached that the name *Achneria* as applied to the South African species is not valid and that the South African genus *Achneria* Munro is not congeneric with the Australian genus *Eriachne* R. Br. although the affinity is very close.

The species formerly placed in *Achneria* Munro are considered to belong to the genus *Pentaschistis* Stapf, and the necessary new combinations and new names are made.

Where new specific names were necessary these should have been designated "Nom. nov." not "Comb. nov."

- 24. van der Bijl, P. A.** "Descriptions of some previously unnamed South African Fungi. II." *S. Afr. Journ. Sci.* **23**, pp. 283-284. 1926. (2. 14.)

The following new species are described: *Meliola zehneriae*, on leaves of *Zehneria obtusiloba* Sond.; *M. cluytiae* on leaves of *Cluytia pulchella* (presumably of Linnaeus); *M. celtidicola* on leaves of *Celtis soyauxii* Engl.; *Eubelonis ocoteae* on the bark of living *Ocotea bullata* E. Mey; *Puccinia drimiae* on leaves of *Drimia pusilla* Jacq.

- 25. van der Bijl, P. A.** "List of Fungi recorded from the Pietersburgtanean Area of the Transvaal." *S. Afr. Journ. Sci.* **23**, pp. 285-289. 1926. (2. 15.)

A list of fungi from the Knysna district is given, containing 124 species belonging to 58 genera and to 26 families arranged alphabetically under their respective families.

- 26. Verwoed, L.** "Adisionele beskrywings van enkele Suid-afrikaanse Gastromycetes." *S. Afr. Journ. Sci.* **23**, pp. 290-294. 1926. (2. 16.)

Descriptions are given of new species of *Arachnion*, *Geaster*, *Lycoperdon*, *Scleroderma* and *Sclerogaster*.

- 27. Saunders, A. R.** "Some Aspects of the Virus Disease Problem in Plants." *S. Afr. Journ. Sci.* **23**, pp. 295-304. 1926. (2. 17.)

A general account is given of the nature of pathogenic viruses and the effect of environment on virus diseases. The lack of properly organised efforts to control these diseases in South Africa is emphasised and special reference is made to the rosette disease of peanuts, the virus diseases of maize and sugar-cane and the degeneration diseases of the potato, all of which present urgent problems in South Africa.

- 28. Storey, H. H.** "Interspecific Cross-transmission of Plant Virus Diseases." *S. Afr. Journ. Sci.* **23**, pp. 305-306. 1926. (2. 18.)

Transmission from streak-diseased Uba cane was experimentally obtained to Uba cane by use of *Balclutha mbila* Naude as vector, with the production of the normal pattern in the experimental cane plants. Cross-transmission from Uba cane to maize produced a disease similar to normal maize-streak but distinguishable by a very sparse distribution of the chlorotic areas. Infection with the sparse form was found experimentally to confer no immunity to infection by the normal form. In certain instances cane plants were thought to have been infected by the virus from the maize but to have recovered from it.

- 29. Storey, H. H.** "Recent Researches on Plant Virus Diseases." *S. Afr. Journ. Sci.* **23**, p. 307. 1926. (2. 19.)

The author failed to transmit the streak disease of maize by any method of direct inoculation either from diseased maize plants or from crushed infected leaf-hoppers of the species *Balclutha mbila* Naude which is in life a highly efficient vector of the disease. One insect remained infective to maize after four months, during which it fed solely upon healthy sugar-cane but in some instances a definite loss of infective power was demonstrated.

Whereas 70 to 80 per cent. of hoppers obtained the virus after a short period of feeding upon the chlorotic areas of the leaf, less than 15 per cent. became infected from the green portions of the leaf. This partial localisation of the virus to the chlorotic areas of the leaf seems to show similarity to Bauer's infectious chlorosis of the Malvaceae.

- 30. Bremekamp, C. E. B.** "On the Opening Mechanism of the Acanthaceous Fruit." *S. Afr. Journ. Sci.* **23**, pp. 488-491. 1926. (2. 20.)

At the moment of opening the septum in the middle of the fruit splits and allows the valves to separate; the seeds then being flung away by an elastic contraction of the hooklike funicles. The opening itself is brought about by water so that these fruits belong to those called by Ascherson "hygrochastic" in contradistinction to the more common "xerochastic" fruits, which open by desiccation.

Hygrochasy is usually supposed to be a peculiarity of desert plants and to be a feature of great biological importance. The Acanthaceae, however, is a family which is almost confined to mesophytic habitats.

- 31. Naude, T. J.** "Insects in Relation to Plant Disease." *S. Afr. Journ. Sci.* **23**, pp. 644-649. 1926. (2. 21.)

Some of the more important entomological data bearing on the subject of virus diseases are brought together and the various ways in which insects are associated with injuries to plants are classified.

- 32. Du Toit, Alex. L.** *Geology of South Africa*. Pp. i-x + 1-445. With 39 plates, 64 text-figs. and map. Edinburgh: Oliver and Boyd. Price 28s. (2. 22.)

This work contains a considerable amount of information of ecological importance, particularly as regards soil formation and the types of soil met with in South Africa. Climatic and geographical influences in soil evolution are discussed and a classification of the soils of South Africa is given.

The strips of *Alluvium* are nearly everywhere narrow, the largest being the flood-plain of the Zambesi. *Aeolian Sandy Soils* form the Kalahari region and cover an area no less than 40 per cent. of South Africa. *Sedentary Sandy Soils* fall into several well-defined classes

which together cover a very wide area. *Dry Steppe Soils*, known as "Karoo Soils," support a vegetation consisting principally of small bushes (*Pentzia*) and other shrubs of the Karroo flora; grasses being restricted to areas invaded by sand. These soils are very fertile when irrigated. *Brown Soils* are poorly represented owing to the general deficiency of humus. *Black "Cotton" Soils* which are met with in the Central Transvaal, Southern Rhodesia and Portuguese East Africa are known to the Dutch farmer under the name of "Black Turf" owing to the peaty aspect, although the proportion of organic matter is by no means high. Comparison with the "Tschernozem" soils of Russia is thus unsatisfactory. Several classes are very fertile despite the low nitrogen content. *Red Loams* occur typically in Southern Rhodesia but are also found near Pretoria, and in Natal and Zululand. Fertility is often seriously reduced by excess of magnesium compounds. *Lateritic Soils* are known from the territory north of the Zambezi and are also likely to occur south of that river. Poverty in plant food compels trees to send their roots deep down in order to reach deeper seated and less decomposed rock material.

The general dependence of soil character upon the solid geology is true to the extent that over wide stretches in Rhodesia and the Transvaal the geological boundaries can be mapped very largely by means of the soil characters. The dependence of a sedentary soil upon the rock which it overlies and from which it has been derived is, however, true only in a certain degree, because the geological formation merely provides the soil material from which the soil becomes evolved under the influences of position, climate and organic life. Almost identical soils can, under special circumstances, arise from radically dissimilar geological formations.

Not every soil has been able to attain the final state which is characteristic of its climatic zone and it is probable that in South Africa such imperfectly developed types, in an immature or intermediate stage of development, are quite as abundant as end-product soils. The deficiency of humus explains the general lack of distinction between soil and subsoil.

- 33. Sim, T. R.** "The Bryophyta of South Africa comprising Sphaerocarpaceae, Marchantiales, Jungermanniales, Anthocerotales, Sphagnales, Andreaeales, Polytrichales, Bryales." *Trans. Roy. Soc. S. Afr.* **15**, pp. 1-475. 1926. (2. 23.)

This work, the result of thirty-five years study of the South African Bryophyta, provides a complete monograph with keys to the various groups, genera and species, followed by careful descriptions and many illustrations in the text. Fifty-four families, 224 genera and 671 species are dealt with. Collectors' numbers are quoted and the habitat and distribution indicated. A number of new species are described in the work and a historical introduction and short bibliography are also included.

(3) AUSTRALIA (COLLABORATOR, V. S. SUMMERHAYES)

- 34. Cambage, R. H.** "Notes on the Native Flora of New South Wales, Part XI. Moree to Mungindi and Moonie River." *Proc. Linn. Soc. New South Wales*, Sydney, **51**, pp. 315-326, Plates XVIII-XXII, 1 map in text. Sept. 15th, 1926. (3. 1.)

The writer describes a visit to part of northern New South Wales on the upper course of the Darling River explored by Major T. L. Mitchell in 1832. The rainfall though small is more than twice as much as in western New South Wales and consequently the vegetation

is fairly luxuriant. The country is practically level and on the whole well-wooded with open plains at intervals. Sandy patches occur locally and these support a vegetation distinct from that elsewhere. Notes on the habitats of many of the species are given.

- 35. McLuckie, J. and Petrie, A. H. K.** "An Ecological Study of the Flora of Mount Wilson. Part III. The Vegetation of the Valleys." *Proc. Linn. Soc. New South Wales*, Sydney, **51**, pp. 94-113, Plates VIII-X, 6 figures in the text. July 1st, 1926. (3. 2.)

The study of the vegetation of Mount Wilson is continued by an enquiry into the distribution of the plant communities in the valleys and on the valley slopes. On the sheltered south and south-east slopes the *Ceratopetalum-Doryphora* association continues down from the basalt caps into the bottom of the sandstone valleys. In the more exposed sandstone valleys the association is confined to the creek bed at the bottom. Migration of the rain forest up erosion channels on the slopes of such valleys is recorded. A comparison of the rain forest on the sandstone and on the basalt follows, with suggested interpretations of the outstanding differences.

The *Eucalyptus goniocalyx-E. Blaxlandi* association is represented fragmentarily along the edge of the rain forest in the bottom of the more exposed gullies. It is also extensively developed on the sandstone below the basalt on north-east and east slopes. A *Eucalyptus oreades* consociation occurs on spurs of certain south-east slopes towards Mount Irvine; this seems to be a more mesophilous expression of the *Eucalyptus goniocalyx-E. Blaxlandi* association. Northern and western valley slopes are occupied by the *Eucalyptus piperita* consociation which extends actually on to the edge of the basalt at the top of the slope. The *E. haemastoma* var. *micrantha* consociation occurs on a small spur projecting in a westerly direction on a south-westerly slope. A discussion on succession follows, together with some observations on semi-natural vegetation.

For a more detailed notice of this paper see *Journal of Ecology*, **15**, p. 174, and of Parts 1 and 2 of the same study see **14**, pp. 357-358.

- 36. Clarke, E. de C.** "Natural Regions in Western Australia." *Journal Royal Society of Western Australia*, Perth, **12**, pp. 117-132, 1 map. July 30th, 1926. (3. 3.)

Western Australia can be divided firstly into two major physical divisions, namely (1) a low-lying strip running along the coast from Albany to Broome, and (2) a tableland occupying the interior. Geologically the state can be divided into eight areas and these again can be subdivided according to climate, chiefly rainfall. As a result fifteen natural regions are obtained, three in the coastal belt and the remaining twelve on the plateau. A table giving the geological and climatic distinctions of these regions is given. The regions are then taken serially and are described in detail with notes on vegetation and possible future development. A useful list of references to the sources of information is provided.

- 37. Hall, L. D.** "The Physiography and Geography of the Hawkesbury River between Windsor and Wiseman's Ferry." *Proc. Linn. Soc. New South Wales*, Sydney, **51**, pp. 555-593, Plates XXXV and XXXVI, and 18 figures in the text. December 15th, 1926. (3. 4.)

A short account of the vegetation of the district studied is given. The geology and climate are fairly uniform, resulting in a great similarity in vegetation types. Various species of

Eucalyptus seem to be the most important trees. On the higher ridges the poor dry sand-stone soil supports a xerophyllous flora composed chiefly of *Eucalypts*, *Proteacæe* and *Leguminosae*. In the most sheltered valleys rain forest of *Ceratopetalum apetalum*, *Callicoma serratifolia*, etc., occurs, while in shallower valleys intermediate types of forest are found.

38. Rodway, F. A. "Some Ecological Features in Tasmania." *Report of Australasian Assoc. for Advancement of Science*, Sydney, 17, pp. 730-738. 1926. (3. 5.)

Considering the small size of Tasmania it possesses great extremes of climate in different parts. The annual rainfall varies from 100-150 in. (2560-3820 mm.) on the west coast to 25 in. (640 mm.) in the midland plains and only 14 in. (360 mm.) on the east coast. This has a great influence on the plants, for instance species which at Hobart can only live above 3000 ft. (900 m.) descend to sea level in the west. The island is very mountainous, with high plains at 1000 ft. altitude in the centre. In spite of this the whole of the country, with the exception of the rocky peaks of the mountains, lies within the tree limit, and is usually well forested.

The forests are mainly of *Eucalypts* of which there are many species, different species being dominant at different altitudes. Below 2000 ft. the chief species are *Eucalyptus globulus*, *E. amygdalina*, *E. viminalis*, *E. obliqua* and *E. ovata*, these being replaced at 2000 ft. by *E. muelleri* and *E. urnigera* which only form a narrow belt of woodland. At 3000 ft. *E. gunnii* and *E. coccifera* take the place of the last-named species and form forests up to the tree limit. The *Eucalypts* form a very light type of forest owing to their vertically hanging leaves, and consequently there is usually a subsidiary tree layer composed of *Nothofagus*, *Atherosperma* and species of *Acacia*, under which there is a shrub layer. In the south-western parts the shrub layer is so dense as to be practically impenetrable. The shrubby plants are of a xerophyllous type, frequently possessing thick leathery leaves and sunken stomata, but can often live only where abundant supply of water is available; this is probably due to the dry air and intense insolation during certain periods.

Grasslands occur in the areas with less rainfall and also in certain other places, one of the chief grasses being *Poa caespitosa*. On glacial deposits or on acid rocks wet acid peat is produced and here the cyperaceous *Mesomelaena sphaerocephala* forms extensive communities, while on wet clay soils *Gahnia psittacorum* dominates.

At about 4000 ft. alpine communities replace the forest. Many shrubs such as *Leptospermum*, *Baeckea* and *Eucryphia* here occur in procumbent forms, while the dwarf conifers *Podocarpus alpina* and *Microcachrys tetragona* are interesting plants of this region. Cushion plants are very abundant, the three most important species being *Abrotanella forsterioides*, *Donatia novae-zelandiae* and *Dracophyllum minimum*, these being almost indistinguishable except when in flower. The rainfall is high and bogs abound, often containing *Sphagna* of which *S. subbicola* is the chief species.

Halophytic communities are found in the estuaries of the Derwent and Tamar and also on the north-west coast. At lower levels *Zostera marina*, *Halophila ovalis*, *Salicornia australis*, *Ruppia maritima* and *Potamogeton pectinatus* all form communities, while on the high mud-flats *Juncus maritimus* and *Phragmites communis* occur, with other marsh plants. In fresher water *Heleocharis sphacelata* and *Triglochin procera* are abundant.

Sand dunes occur in a number of places, being naturally stabilised by the grasses *Spinifex hirsutus*, *Poa billardieri* and *Schedonorus littoralis* together with *Scirpus nodosus* and also the woody *Myoporum serratum* and *Acacia sophorae*. This natural community has been destroyed by fire in places and here travelling dunes may be found.

(4) NEW ZEALAND (COLLABORATOR, V. S. SUMMERHAYES)

- 39. Cockayne, L.** "Monograph on the New Zealand Beech Forests, Part I. The Ecology of the Forests and Taxonomy of the Beeches." *New Zealand State Forest Service, Bull. No. 4*, Wellington, pp. 1-71, 26 half-tone plates, 9 figures in the text, 2 maps. 1926. (4. 1.)

The primary object of the monograph is to ascertain if New Zealand beech forests can be profitably dealt with as a perpetual source of timber supply.

Reasons are given for classing all New Zealand forests as rain forest, but this must be divided into (1) subtropical rain forest, or rain forest proper, and (2) subantarctic rain forest, to which belong all classes of beech (*Nothofagus*) forest. The following five species are recognised: *Nothofagus menziesii*, *N. fusca*, *N. truncata*, *N. solandri*, *N. cliffortioides*. There are a vast number of hybrids, all the species, except *N. menziesii*, being concerned. Included in the hybrids are *N. blairii* and *N. apiculata*, formerly considered species. The species have each a different altitudinal range, but *N. truncata* and *N. solandri* are confined to the lowland-lower montane belt, and *N. cliffortioides* ascends to above the timber line as a low shrubby tree. *N. menziesii* frequently forms the uppermost belt, but only if *N. cliffortioides* is absent. From the standpoint of tolerance of drought *N. fusca* is the most mesophytic, and *N. cliffortioides* the most xerophytic.

The rainfall necessary for the establishment of beech forest is the same as that for rain forest proper, except that certain mountain-beech associations can do with rather less. The tussock-grassland climate is unfavourable for natural establishment of forest, not merely because the rainfall may not be sufficient, but because the winds are too frequent, too violent, and, in some places, too hot. Beech forest is indifferent to the chemical composition of the soil, except in the matter of excess of salt or magnesia. Extremely wet soil may lead to the formation of bog rather than forest, as in certain parts of the Fiord district. Beech forest usually occupies much poorer soil than rain forest proper. Possibly the present distribution of *Nothofagus* forest in New Zealand can be referred to its competition with rain forest proper, the latter having driven it on to the poorer ground or to the higher altitudinal belts; while events at the close of the glacial period may account for the absence of beech forest on the Westland coastal plain and the mountains adjacent.

As time goes on, the forest makes its own climatic and edaphic conditions for its members. The moist atmosphere of the forest is of moment mainly with regard to the undergrowth, for the beeches themselves remain in vigorous health under quite dry atmospheric conditions when the majority of the trees and all undergrowth has been removed. The light factor is of supreme moment in regard to the composition of the undergrowth. Excess of light encourages seedlings in general to develop, but the amount of light is governed less by the roof canopy than by the undergrowth, each species of which has its special light-reducing power. Thus the composition of the undergrowth is a main factor with regard to the nature and rapidity of succession. The maximum of light is indicated by the incoming of bracken. Other species indicate a rather less bright light—e.g. wineberry, lawyer, the species of beech and *Parsonia heterophylla*. The bryophyte and filmy-fern carpet of the floor is of great value on account of its moisture-holding power and its function as a seed bed.

With increasing altitude the trees become smaller, and at the highest altitude subalpine shrubs enter the forest; but in the southern districts these also come into the lowland belt. Competition is a powerful factor with regard to the composition and structure of forest. The more dense the growth form, the more certain is the possessor of not being molested by seedlings developing under its shade. In this regard certain fairly large close-growing

ferns come first. A relatively rapid rate of growth from the seedling stage onwards is responsible for the dominance of many species. Those of *Nothofagus* stand very high in this regard. Certain species grow exceedingly slowly within the forest and can linger for many years—e.g. *Podocarpus hallii*—but, if bright light is let in, vigorous growth very soon takes place. Grazing and browsing animals have profoundly modified the forest composition and structure, and brought about changes almost beyond belief. The following are some of the new destructive features these animals have directly and indirectly caused: (1) reducing greatly the water content of the soil; (2) destroying the all-important seed beds; (3) causing erosion to a remarkable degree; (4) killing seedlings; (5) altering or forbidding succession; (6) destroying absolutely various species of trees and shrubs, including beeches and totaras.

A classification is put forward based on latitudinal and altitudinal changes, relative rainfall, and the dominant species of *Nothofagus*. Beech forest is usually a community composed of massive evergreen trees varying in height from 70 ft. or more to 20 ft. or less at the timber line. There is always a certain amount of shrubby undergrowth, together with colonies of some four species of fair-sized ferns. Many characteristic features of rain forest proper are either wanting or but little developed—e.g. colonies of tree ferns, liane entanglements, asteliads or shrubs as epiphytes, fair-sized trees rising above the shrubby undergrowth. The forests of many localities are described, from that of Mount Te Aroha in the north to those of the Fiord and South Otago districts in the south.

Regeneration is divided into: (1) natural regeneration of standing forest; (2) regeneration after milling; (3) reinstatement after burning. Also regeneration after grazing and browsing animals are removed is considered. The following fundamental facts must be stressed: (1) that all the species of *Nothofagus* require for their rapid development more light than is provided by the average forest canopy, and (2) that development in full light outside the forest is at least three times as rapid as in a well-lit forest interior. In every piece of mature beech forest visited regeneration was more or less clearly in progress. In forests where taxads are also present these, when they fall, are in many localities replaced by beech. After milling, the ground is generally occupied in a comparatively short time by thickets of beech saplings. Forest which has had the undergrowth completely destroyed by grazing and browsing animals rapidly produces new undergrowth when these are removed. When the forest has been entirely destroyed by fire, and there are no beech trees in the immediate neighbourhood, there is no reinstatement, but if isolated living beech trees remain dense thickets of beech soon arise in their vicinity. In some localities beech forest is extending its area on to tussock grassland, even when a few grazing animals are present. Manuka (*Leptospermum scoparium*) and beech often develop together in the open. For a time they grow at about the same rate, but in a few years the beech overtops the manuka, cuts off the light, and completely kills it. In this manner beech forest frequently commences.

40. Allan, H. H. and Dalrymple, K. W. "Ferns and Flowering Plants of Mayor Island, New Zealand." *Trans. New Zealand Institute*, Wellington, 56, pp. 34-36, 1 plate. March 6th, 1926. (4. 2.)

Mayor Island lies in the Bay of Plenty on the north coast of New Zealand. The island is volcanic in origin, rising to 400 m. in the north, and with two crater lakes in the centre. The chief tree is *Metrosideros tomentosa*, which forms woodland on the lower flatter areas. In the hills *Leptospermum scoparium* and *L. ericoides* dominate on the dry spurs, *Entelea arborescens* is the chief plant in the gullies, while on the slopes *Aristotelia serrata* and other trees form a mixed community. Exotic plants are frequently found and in places form definite communities following cultivation. A list of species is given.

- 41. Cockayne, L. and Allan, H. H.** "The Present Taxonomic Status of the New Zealand Species of *Hebe*." *Trans. New Zealand Institute*, Wellington, **57**, pp. 11-47. October 9th, 1926. (4. 3.)

In this paper the authors deal with the genus *Hebe* (*Veronica* sect. *Hebe* Benth.) along the lines advocated in their recent paper in the *Journal of Ecology* (**15**, No. 2, pp. 234-277; 1927), and analyse the compound species as far as the data permit. It is suggested that a number of the described "species" are either natural hybrids or are habitat forms.

- 42. Wall, A.** "Some Problems of Distribution of Indigenous Plants in New Zealand." *Trans. New Zealand Institute*, Wellington, **57**, pp. 94-105, 10 diagrams in the text. November 17th, 1926. (4. 4.)

The distribution of species is often very peculiar or discontinuous. About fifty cases of species with such distribution are tabulated and these are divided into seven classes according to the relation between the distributions of the species and those of their nearest relatives. The ways in which these might have arisen are then discussed, and it is suggested as an explanation of "isolated" species that all the individuals of a given species in a certain area may have changed into a new species by mutation or in some other way.

- 43. Allan, H. H.** "The Vegetation of Mount Peel, Canterbury, New Zealand." *Trans. New Zealand Institute*, Wellington, **56**, pp. 37-51. March 6th, 1926. **57**, pp. 73-89. November 13th, 1926. (4. 5.)

The area described consists of a group of mountains rising to a height of 1740 m., with an area of over 42 square miles. The rather soft Greywacke rock weathers readily into rocky peaks and slopes. The average annual rainfall of the district is about 1100 mm., but may be only 900 mm. in the higher regions. The broad features of the vegetation are due to the interaction of four main factors, viz. Topography, Climate, History during and since the Glacial Period, and the underlying rocks.

The forests, which occur on the lower slopes, can be divided into (a) rain forest, and (b) southern beech forest dominated by *Nothofagus cliffortioides*. There are two types of rain forest, firstly, that of the flood plains and terraces with *Podocarpus dacrydioides*, *P. spicatus* and *P. totara* in varying proportions according to edaphic conditions, and secondly, a mixed type on the slopes in which the Podocarps are infrequent, while a number of other trees are co-dominant. Both types rejuvenate readily after fire provided grazing animals do not obtain access. The beech forest occurs only at higher altitudes, especially in the northern parts of the region, and seems to be dying out. Since its first establishment after the glacial period it has probably been replaced by the rain forest owing to an increase in the rainfall.

Scrub occurs frequently as a seral unit, either in primary successions on river terraces or on screes, e.g. *Coprosma propinqua*, *C. parviflora*, *Discaria toumatou*, or in secondary successions following burning of grassland or forest, e.g. *Leptospermum scoparium*. In other cases scrub occurs as the climax community in places with intermediate exposure such as *Dracophyllum* spp. on steep slopes, while there is also a narrow belt of mixed scrub on the upper margins of the forest belt.

The grasslands occur usually above the forest areas and are climax communities due to exposure. Two main divisions can be recognised, namely, low tussock grassland (600-1000 m.), consisting chiefly of *Poa caespitosa* and *Festuca novae-zealandiae*, and tall tussock grassland (700-1300 m.), in which the dominant plant is *Danthonia flavescens*. Grassland is usually first met with at about 600 m., but on shaded slopes tall grassland may descend

to 300 m. The distributions of the two types are determined by the duration of the winter snow. Following severe burning or grazing, especially in the low grassland, exotic species become very abundant or even dominant, e.g. *Verbascum thapsus* in rabbit-infested areas. These aliens are less abundant in the tall tussock grassland, which on burning is converted into "fell-field" (fjældmark). In flushed areas in both types of grassland species of *Juncus* and *Carex* form special communities.

Above the grassland the only communities are types of fjældmark of which two are important. On steeper slopes *Celmisia lyallii* is characteristic together with *Danthonia flavescens*, while *C. viscosa* occupies the flatter ground, often associated with *Dracophyllum rosmarinifolium*. The communities are quite open with much rock debris, the duration of the snow covering being the chief differentiating factor. When burnt *Celmisia lyallii* is replaced by *Poa colensoi*. On more unstable places, such as shingle slips, *Poa sclerophylla* and *Ranunculus haastii* are the chief species. On the summits definite rock inhabiting communities are found, these varying locally with insolation and water supply, and including a great number of species, of which twelve are found only on rocks in the Mount Peel district.

Of the exotic plants *Ulex europaeus* forms definite communities both on the river shingle and on the slopes up to 550 m. In well-developed *Ulex* scrub, *Holcus lanatus* and *Anthoxanthum odoratum*, both aliens, are the chief species.

- 44. Cockayne, L. and Allan, H. H.** "Notes on New Zealand Floristic Botany, including Descriptions of New Species, etc. (No. 5)." *Trans. New Zealand Institute*, Wellington, **57**, pp. 48-72. October 9th, 1926. (4. 6.)

Includes notes on exotic species wrongly included in the flora of New Zealand, and additions to our knowledge of the geographical distribution and ecology of some native species.

- 45. Laing, R. M.** "A Reference List of New Zealand Marine Algae." *Trans. New Zealand Institute*, Wellington, **57**, pp. 126-185. November 17th, 1926. (4. 7.)

- 46. Grimmett, R. E. R.** "Forest-floor Covering and its Life." *Trans. New Zealand Institute*, Wellington, **56**, pp. 423-440. April 10th, 1926. (4. 8.)

The litter covering the floor of a forest supports a varied fauna which plays a definite part in the reduction of the vegetable material to a form available for plants. Two localities, one in beech forest (*Nothofagus solandri* and *N. fusca* co-dominant) and the other in tawa forest (*Beilschmiedia tawa*, etc.), were studied by taking samples and analysing the fauna found, together with observations on habits. The occurrence and frequency of the various taxonomic groups is dealt with briefly. As regards individuals, saprophagous species by far outnumber the phytophagous species. In general characters the communities agree in the two types of forest, but specifically there are many differences. Comparisons with similar investigations in other countries are given.

- 47. Thomson, G. M.** "The pollination of New Zealand Flowers by Birds and Insects." *Trans. New Zealand Institute*, Wellington, **57**, pp. 106-125. November 15th, 1926. (4. 9.)

Notes on the birds and insect visitors of over 100 species of the New Zealand flora are given, and the need for further observations is emphasised.

48. Myers, J. G. "Biological Notes on New Zealand Heteroptera." *Trans. New Zealand Institute*, Wellington, 56, pp. 449-511, Plates 81-86 and 26 figures in the text. April 26th, 1926. (4. 10.)

Many notes on the host-plants of the various species of New Zealand Heteroptera are given in this paper. *Ulex europaeus*, *Cytisus scoparius* and *Crataegus monogyna*, which are the host plants of a large number of bugs in Europe, are completely free from these parasites in New Zealand. Many species of Heteroptera feed on conifers in Europe, but the native New Zealand species are but rarely attacked.

49. Allan, H. H., Simpson, G. and Thomson, J. S. "A Wild Hybrid *Hebe* Community in New Zealand." *Genetica*, 8, pp. 375-388, 2 plates, 1 figure in the text. 1926. (4. 11.)

A scrub community of *Griselinia littoralis* is described in which *Hebe salicifolia* var. *communis*, *H. elliptica* and various hybrids between them are abundant, a list of associated species being given. The production of the hybrids has been much aided by partial destruction of the original scrub. The *Hebe* hybrids are analysed and their relation to the two parents indicated in a tabular manner. The whole series is given the name \times *Hebe elliptica* Cockayne and Allan; and the identity of some of these forms with certain described "species" is suggested. The importance of such hybrid swarms in both taxonomy and ecology is stressed.

(5) PACIFIC ISLANDS (COLLABORATOR, V. S. SUMMERHAYES)

50. Setchell, W. A. "Phytogeographical Notes on Tahiti. I. Land Vegetation." *University of California Publications in Botany*, Berkeley, Calif. 12, No. 7, pp. 241-290. August 21st, 1926. (5. 1.)

Tahiti is one of the most easterly of the volcanic islands in the Pacific, the nearest "high" islands being over 300 miles away. Around the island is a narrow coastal plain while inland the mountains rise steeply to over 7000 ft. (2100 m.), the slopes being cut up by deep and narrow valleys. The soil is decomposed volcanic rock mixed with coral rock in the coastal areas, and is quite shallow and rather deficient in "humus."

The temperature is relatively uniform, and snow is apparently unknown: The annual rainfall varies from 40-130 in., but records are not available from the wettest places. The upper slopes are usually covered with cloud or mist.

On the coastal plain and on the lowermost slopes the communities are nearly all secondary, being composed, outside cultivation, chiefly of weeds or planted shade trees. Of the weeds *Lantana camara* and *Psidium guajava* form extensive thickets while *Elephantopus mollis* and *Bidens pilosa* are troublesome herbs. On the coast itself mangroves are missing although favourable localities occur, but many common Polynesian strand plants occur. On sandy coastal areas *Ipomaea pes-caprae* is dominant while at higher levels *Canavalia microcarpa* and *Vigna marina* occur.

The slopes may be divided into two parts, the ridges and the valleys. The ridges support a xerophytic community of *Dicranopteris linearis* ("*Gleichenia dichotoma*") up to 5000 ft. (1500 m.), the plants forming a dense thicket 10 ft. or more in height. *Dodonaea viscosa* and *Metrosideros collina* occur occasionally while the lower slopes are being invaded by the American shrub *Stenolobium stans*. Above 5000 ft. the scrub becomes lower and consists mainly of the xerophytic *Lycopodium cernuum* and *L. volubile*, but little is known of this region. In damper hollows *Fitchia nutans* is found.

In the valleys the plains flora is found up to 1000-1800 ft. on the drier side of the island, but above this is forest, which descends nearly to sea level in the wetter regions. These forests fill the valleys, which are very humid, up to 3000 ft. (900 m.). In these forests are found most of the indigenous species of Tahiti and a very mixed flora occurs.

The relationships of the flora are discussed in the second part and also the various means of dispersal of the plants. The importance of considering the various factors, climatic, edaphic and biotic, affecting ecesis and persistence is stressed.

51. Setchell, W. A. "Phytogeographical Notes on Tahiti. II. Marine Vegetation." *University of California Publications in Botany*, Berkeley, Calif. 12, No. 8, pp. 291-324. August 21st, 1926. (5. 2.)

No marine spermatophytes are known from Tahiti, the other Society Islands, Marquesas Islands or Rarotonga. The known marine algae of Tahiti are practically all of the littoral zone, with the exception of some Melobesia and Squamariaceae. The different ecological forms and ecological behaviour of the Tahitian marine algae are the same as was determined for the marine algae of Tutuila and of Rose Atoll.

The calcareous crustaceous algae (nullipores) are primarily concerned in building up the "coral reefs." The reefs of Tahiti may be classified as barrier reefs, exposed fringing reefs, and protected fringing reefs. There exist on the shores of Tahiti "barrier banks" similar in position to the barrier reefs, and these may develop into barrier reefs.

The barrier reefs are covered mainly by a pavement of *Porolithon onkodes* which is about 200 ft. wide and extends to a depth of 6 ft. on the seaward side. On the inside of the central ridge is a zone of *Sargassum sociale* and *Turbinaria ornata* about 50-60 ft. wide, growing on the *Porolithon*. The exposed fringing reefs are also covered with *Porolithon* and are similar to the barrier reefs in many respects. On the protected fringing reefs the calcareous algae are covered with a thin layer of silt on which are found *Caulerpa sertularioides* and species of *Polysiphonia*, *Dictyota*, *Padina*, *Cladophora* and *Enteromorpha*. The second conspicuous reef-former of the Indo-Pacific region, the fruticulose branched *Porolithon craspedium*, although credited to Tahiti, could not be found, and is probably characteristic of atolls.

52. Riley, L. A. M. "Notes on the Flora of Rapa." *Kew Bull. Misc. Inform.*, London, 1926, pp. 51-56, 1 map. March 1st, 1926. (5. 3.)

Rapa is an isolated island 250 miles south-east of the Austral Islands, and is of volcanic origin, rising to over 2000 ft. (600 m.). The hill slopes are covered with grass and ferns, but there are woods in the gullies in which the chief tree is *Aleurites moluccana* at the lower levels, while above 150 m. a tree fern gradually assumes dominance. An interesting plant in the lower forest is the arboreal composite *Fitchia nutans*. The flora is very poor but of some phytogeographical significance.

(7) INDIA, BURMA AND CEYLON (COLLABORATOR, J. R. MATTHEWS)

53. Lewis, F. "The Altitudinal Distribution of the Ceylon Endemic Flora." *Ann. Roy. Bot. Gard. Perad.*, Ceylon, 10, Pt. 1, pp. 1-130. June, 1926. (7. 1.)

In this paper the author gives an account of the endemic flora of Ceylon, exclusive of cryptogams, and presents in tabular form a full list of the species peculiar to the island showing their altitudinal range for every 1000 ft. up to 7000 ft. The table is based largely upon data taken from Trimen's *Flora of Ceylon*. To illustrate the differences in distribution between east and west the island is divided roughly into two regions by a line running

approximately north and south from the Trigonometrical Station on Pidurutalagala (8292 ft.)—the highest point in Ceylon. Of the 149 families represented in the island flora 89 have endemic species, the total number of endemics being 804. Details of the vertical distribution of 787 of these are given for eastern and western sections of the island. From the western area 721 species are recorded; from the eastern side only 66. In the west 195 species (27 per cent.) are found at elevations not exceeding 1000 ft. while the corresponding figure for the east is 32 or almost 50 per cent. of the total number recorded from that part of the island. Again, while as many as 92 species reach 7000 ft. or over in the west, only one species, *Symplocos cordifolia*, attains this altitude in the eastern part of the island and only 18 species reach an altitude of 6000 ft.

The author emphasises the imperfection of the data at his disposal, yet the remarkable differences which his analysis brings out would seem to have some significance. Various factors affecting the altitudinal range of the endemic flora are discussed and much importance is attached to rainfall distribution. There are few places in the world where such great variation in rainfall occurs as in Ceylon, especially in the western half of the island. Rainfall distribution reacts upon human operations and considerable importance is attached to the influence of man in altering the natural distribution of plants, at the same time adding to the complexity of the problem. Reference is made to the operation of "Chena Cultivation" which consists of cutting down the forest or jungle before the rains, burning, and growing in a most primitive manner such crops as the people require for food. Much vegetation is thus destroyed, the land is in no way conserved against denudation and is abandoned when the crop has been secured, unless the so-called cultivator is pleased to cut down the secondary growth to repeat the operation again.

After referring to other factors which affect the dispersal of plants, the author reviews the several families of flowering plants which possess endemic species in Ceylon. Certain families presenting complex problems as to the distribution of their members are selected for special treatment. The Dipterocarpaceae, for example, with three genera—*Doona*, *Stemonoporus* and *Monoporandra*—peculiar to the island, is distinctly Malayan, yet is essentially western in Ceylon. The Leguminosae, comprising 207 species, has 12 endemics. A contrast is made between this family and the Rubiaceae with 138 species of which as many as 71 are endemic. It is suggested that the pronounced endemism exhibited by the Rubiaceae may be related to the fleshy character of the fruit, attractive to birds, thus leading to wider dissemination. Of the 78 species of Compositae 19 are endemic, all wind-carried, and more occur in the hill country than in the plains. Of the 39 species of Asclepiadaceae, on the other hand, there are seven endemics, also with wind-borne seeds, but only one species ascends to over 4000 ft. The Orchidaceae with 161 species has 78 endemic but the author is unable to suggest any particular reason for the large number of endemic forms in this family. The small family Eriocaulonaceae with 18 species, of which seven are endemic, is interesting since four of these endemics occur below 1000 ft. while the remaining three, all western, occur only above 5000 ft. The Gramineae, the largest family in Ceylon, comprises 240 species with 31 endemics. They have considerable diversity in distribution in contrast to the Cyperaceae, of which only 12 out of 161 species are endemic, most of them being lowland. Only one species of *Carex* ascends to 7000 ft.

Analysis of the data presented by the author shows that the greater number of endemics are to be found at the foot of the hills, not at the higher altitudes. The author suggests that this is explained by gravitational action, "by which streams carry down seeds or fruits that in turn over-populate the lower levels, and in so doing set up a larger struggle for existence; and by the operation of the law of natural selection, the strugglers develop latent forces, that in turn become specifically divergent, and consequently evolve a type, so modified as not only to survive, but to constitute a distinct form. This 'form,' owing to its divergence, we class as a distinct or endemic species."

54. **Biswas, Kalipada.** "Flora of the Salt-Lakes, Calcutta." *Journ. Dept. Science*, 8, pp. 1-47, Plates 1-10. Calcutta University Press. 1926. (7. 2.)

Although phanerogamic vegetation is not excluded, this paper is devoted chiefly to a systematic account of the algal flora of the Indian salt-lakes. The lakes are formed of a considerable number of depressions filled with saline water and surrounded by, or alternating with, extensive stretches of marshy lands. They are situated south-east of Calcutta and cover an appreciable part of the Gangetic Delta. The vegetation of the embankments and bunds of the salt-lakes proper and of the surrounding swamps is briefly described. Three zones of vegetation are recognised, representing in the restricted sense the Mangrove formation of the Sunderbunds farther south. In the vegetation of the swamps and drier lands three storeys are distinguished, the first being composed of microphytes, especially species of *Oscillatoria*. The second storey comprises *Suaeda maritima* and other dwarf flowering plants, while *Avicennia officinalis* and *Aegiceras majus* are the important members of the third and tallest storey. In the lakes themselves, owing to the muddy condition of the water, the constant deposition of silt, the salinity of the water and the action of the tide, there is a striking absence of phanerogams, but algae are abundant, especially Cyanophyceae and Diatomaceae. Certain species of *Oscillatoria* grow most luxuriantly during the rains, and during hot weather *Pandorina morum* and *Enteromorpha prolifera* are very common, but the problem of periodicity in the growth of these plants has not been pursued.

55. **Carter, Nellie.** "Freshwater Algae from India." *Records Botanical Survey, India*, 9, No. 4, pp. 263-302, Plates I and II. Calcutta, 1926. (7. 3.)

This is a systematic account of algae collected by Mr J. H. Burkill at various times between 1906 and 1912, chiefly near the North-Eastern frontier, in North Cachar, the Assam plains and in the Sikkim and Abor Himalayas. The Indo-Malayan type of Desmid is apparently confined to the comparatively low-lying districts of the area, and altitude appears a determining factor in the distribution of Desmids just as in higher plants.

56. **Dixon, H. N.** "Mosses collected in Gilgit, etc., by J. Garrett and W. Lillie." *Records Botanical Survey, India*, 9, No. 5, pp. 303-313, Plate I. Calcutta, 1926. (7. 4.)

A record of mosses collected in the most northerly district of the State of Kashmir. Six species are described and figured as new.

57. **Calder, C. C., Narayanaswami, V. and Ramaswami, M. S.** "List of Species and Genera of Indian Phanerogams not included in Sir J. D. Hooker's *Flora of British India*." *Records Botanical Survey, India*, 11, No. 1, pp. 1-157. Calcutta, 1926. (7. 5.)

This catalogue is arranged in alphabetical order, the entries including all species and genera which have been described as new during the period 1906-1924. The place of publication is given for each species along with a note indicating the geographical range.

58. **Fischer, C. E. C.** "Loranthaceae of Southern India and their Host Plants." *Records Botanical Survey, India*, 11, No. 1, pp. 159-195, Plates 1-4. Calcutta, 1926. (7. 6.)

The author records his observations, extending over twenty years, on the host plants

affected by members of the Loranthaceae. Tubeuf's view that there are in Europe three races of *Viscum album* differentiated only by the host plants they affect is not supported by field observations of the parasitic Loranthaceae in Southern India. Experimental data, however, are lacking. Many genera considered immune by earlier writers are extensively parasitised. The majority of the host plants, of which 274 have been noted, are trees or shrubs, but seven are themselves loranthaceous parasites and two are herbs. *Santalum album*, itself a parasite, is affected by five species of *Viscum*. Appendices to the paper give (1) a list of parasites and their host plants, (2) a list of host plants and the parasites affecting them, (3) a list of parasites and their hosts observed outside the Madras Presidency.

59. Brühl, Paul. *A Guide to the Orchids of Sikkim*. Pp. xvi and 207. Calcutta and Simla: Thacker, Spink and Co. 1926. Price 5 Rs. (7. 7.)

This is a guide to the identification of those species of orchids found between the Terai and the northern frontier of independent Sikkim including the Chumbi Valley and British Bhutan. The book contains a key to the genera and a key to the species.

60. Brühl, Paul, and Biswas, Kalipada. "Algae of the Loktak Lake." *Memoirs Asiatic Society, Bengal*, 8, No. 5, pp. 257-316, Plates 7-22. Calcutta, 1926. (7. 8.)

The Manipur Valley in Assam forms a flat swampy plain about 50 miles long by 25 miles broad at an elevation of about 2600 feet. Loktak Lake lies in the southern part of this valley, but at no time is it more than a large deep swamp, the vegetation of which is extremely luxuriant. The leaves and stems of the submerged plants are as a rule densely covered with small algae. The algal material, of which the authors give a systematic account, was collected by Dr Annandale and Dr Hora. Of the 122 species described and figured, 41 are regarded as new.

Supplement II

BRITISH EMPIRE VEGETATION ABSTRACTS:

TITLES AND ABSTRACTS OF PUBLICATIONS ON THE VEGETATION AND ECOLOGY OF THE OVERSEAS EMPIRE AND ON RELATED TOPICS

(1) CANADA (COLLABORATOR, R. D'O. GOOD)

61. **Svenson, H. K.** "Effects of Post-Pleistocene Submergence." *Rhodora*. 29, pp. 41-48, 57-72, 87-93, 105-114. 1927. (1. 11.)

It is generally believed that, at the end of the last glacial period, there was a marine transgression, the Champlain submergence, into the low-lying area adjacent to the retreating ice. The sea is thought to have covered parts of the marine Provinces of Canada, to have deposited marine beds in river valleys of eastern New England, and what is now Lake Champlain was occupied by an arm of the sea extending as far as the Great Lakes.

It is also well known that a number of plants typical of maritime habitats are to be found over a considerable inland area of eastern North America and the paper abstracted here is an attempt to see how far these facts of distribution are to be correlated with the post-glacial Champlain submergence.

The author begins by giving a short history of his subject and then reviews in some detail the geological evidences for the suggested submergence. This is followed by a detailed and also tabulated account of the inland distribution of the maritime plant species concerned. He then shortly refers to similar phenomena in Europe and their possible correlation with a post-glacial sea.

Next he describes certain salt springs and their flora in the St Lawrence valley and in New Brunswick. A very interesting section of the work deals with the distribution, in the west of the continent, of maritime species found elsewhere in North America only on the Atlantic coast. This leads naturally to a lengthy consideration of the factors, *other than the* Champlain submergence, which may have caused these remarkable distributions.

The writer concludes that maritime plants (halophytes) do not persist inland in eastern North America because of the post-glacial submergence unless salt spring or equivalent conditions are present. None of these plants appear to be confined to the area concerned in the submergence but their inland range is usually confined to low-lying areas adjacent to the sea or to areas with impeded drainage and underlying calcareous rock. Human agencies have perhaps been most effective in distributing the plants.

62. **Criddle, Norman.** "A Calendar of Flowers." *Can. Field Nat.* 41, 3, pp. 48-55. 1927. (1. 12.)

63. **Setchell, W. A.** "*Zostera marina latifolia*: ecad or ecotype?" *Bull. Torr. Bot. Club*, 54, pp. 1-6. 1927. (1. 13.)

64. **Anderson, E.** "*Iris versicolor* in N. Ontario." *Bull. Amer. Iris Soc.* Jan 22nd, 1927. (1. 14.)

- 65. Gisborne, H. T.** "Lightning and Forest Fires in the Northern Rocky Mountain Region." *Monthly Weather Review*, **54** (7). 1926. (1. 15.)

Lightning storms may occur on about 90 days between June 1st and September 30th. In any storm period the earlier storms are more apt to set fires than the later ones, though one storm may set many fires. For the region as a whole, 6 storms out of 10 are declared to be "safe" and 4 out of 10 set fires, although the ratio varies widely in various portions of the region. E. N. Munns, reprinted from *Biol. Abs.* 3374, April 1927.

- 66. Harper, R. M.** "A Six-hour Cross-section of the vegetation of Southern Ontario." *Torrey*, **27**, pp. 1-8. 1927. (1. 16.)

An account of the vegetation as seen from the train during the run from Detroit to Buffalo by way of Canada.

- 67. Adams, John.** *A short guide to Canadian genera of seed plants.* 97 pp. Dominion of Canada, Department of Agriculture, Bulletin No. **78**. New Series. Ottawa. 1927. (1. 17.)

This bulletin consists of 24 chapters dealing with the principal subdivisions of seed plants, the more important families, and all the indigenous genera occurring in Canada. A key arranged on the alternative plan is provided for each of these families and genera, so as to facilitate identification. At the end of each group or family is an alphabetical list of the genera comprised, with the English name, a brief outline of the distribution in the various climatic regions of Canada and an estimate of the number of Canadian species in the genus. In a considerable number of cases the characters of some of the more important species are also described where they are such as to lead to easy recognition of the species. Chapter 23 contains a summary of those genera which fall under special ecologic groups, such as Climbing Plants, Aquatic Plants, etc. Chapter 24 deals with useful plants arranged under the following groups: Edible Plants, Forage Plants, Foods of Wild Ducks and Other Game, Medicinal Plants, Plants that Furnish Timber, Sand-binding Plants, Plants used for Tanning.

(2) SOUTH AFRICA (COLLABORATOR, A. W. EXELL)

- 68. Plummer, F. E.** "A Preliminary Investigation into the Variability of the Rainfall of the Transvaal." (Rainfall and Farming in the Transvaal. Part I.) (2. 24.)

- 69. Leppan, H. D.** "Rainfall in Relation to Agriculture in the Transvaal." (Rainfall and Farming in the Transvaal. Part II.)

Pretoria. *Transvaal Univ. Coll. Bull.* No. **12**. 1927. Pp. 1-63, 17 maps. (2. 25.)

The first part of this paper deals with the amount and reliability of the rainfall of the Transvaal and with its distribution. The records are obtained from a number of stations and extend from 1888 to the present time.

The second part treats of the agricultural possibilities in relation to these results. In the Transvaal the rainfall does not fully meet the needs of agriculture. This is due to several causes in addition to the value of the total precipitation.

The rainfall is concentrated in a short period in the hottest season. Evaporation is very high owing to intense insolation and to wind. Run-off accounts for a considerable loss. This is increased by the heavy storms, the destruction of the natural vegetation, by the

relief, and by the character of the soil in some cases. The transpiration rate is high and the water requirement large. Further, over practically the whole country the rainfall is unreliable, both in amount and in time. The country is divided into five belts determined by the total rainfall. Each of these is subdivided into a northern and a southern part and notes are given on the agricultural possibilities of each.

70. Phillips, J. F. V. "*Faurea McNaughtonii* Phill. ('Terblanz'): A Note on its Ecology and Distribution." *Trans. Roy. Soc. S. Afr.* **14**, pp. 317-336. 1927. (2. 26.)

Faurea Macnaughtonii Phillips (Proteaceae: sect. Persooniadeae) has a markedly discontinuous distribution in southern Africa, occurring in a small area in the Knysna forests, in several isolated stations in the Transkei region, in northern Natal and in one station in the Transvaal.

At Knysna it attains local dominance or sub-dominance. Where dominant the co-dominants are *Podocarpus Thunbergii* Hook. and *Olea laurifolia* Lamk.; where sub-dominant, as is more general, it occurs in the extensively developed *Podocarpus Thunbergii*-*Olea laurifolia*-other spp. association. In the Transkei and Natal the tree is less locally abundant, and is not a dominant in any community. It is a moderately light-demanding tree but is sensitive to insolation in the seedling stage. The tree flowers freely and 40 per cent. to 80 per cent. of the flowers set seed. The germination capacity is, however, low, due apparently to under-development of the seeds and not to parasites or disease. The dispersal of the nuts is over very short distances so that there is an aggregation of regeneration on the crown-influence zones of the parents.

In discussing the discontinuous distribution it is held that the wide-ranging species *F. speciosa* Welw. and *F. saligna* Harv. have been responsible for the appearance of *F. Macnaughtonii* in the Transvaal and in Natal, and that its presence in the Transkei and Gouna (Knysna) are due to *polygenesis* having taken place.

71. Phillips, J. F. V. "Experimental Vegetation: A Second Contribution." *S. Afr. Journ. Sci.* **24**, pp. 259-268. 1927. (2. 27.)

This is an abstract of which the full records are filed at the Forest Research Station, Knysna, giving an outline account of a series of experiments designed to investigate the effects of felling and exploitation of the primeval forests with special reference to changes caused by removal of the forest canopy. Experimental plots were chosen and screened to give initial light intensities of 0.5, 0.2, 0.06 and 0.01 of full sunlight. The plots were cleared and forest soil introduced to a depth of 3 ft. Seeds and seedlings of forest trees were planted.

The results may be summarised as follows:

(1) A light intensity of 0.06 to a forest soil that has had lower values causes an improvement in its permeability and air capacity, renders it less acid and makes the salts more easily available. Weeds are inhibited.

(2) Light values of 0.5 and 0.2 decrease permeability and air capacity. Dense weed growth appears which reduces the soil-moisture and increases the amount of partially decayed humus and the acidity. Ultimately the light-value at the seedling level is seriously reduced.

(3) A light value of 0.01 does not alter the quality of the soil. No weeds appear. The plants produced are very poor.

(4) Initially fast-growing plants are able to compete with the weeds, if given a sufficient start, but slow-growing plants cannot do so and are suppressed in the higher light-intensities.

(5) The experiments support at all points the results of earlier work. Exposure of forest soil is detrimental to the soil itself and so inhibits the establishment, development and growth of forest regeneration.

- 72. Phillips, J. F. V.** "*Ekebergia capensis* Sparrm. ('Essenhout') in the Knysna Region: A preliminary Ecological Note." *S. Afr. Journ. Sci.* **24**, pp. 216-224. 1927. (2. 28.)

Ekebergia capensis Sparrm. (Meliaceae: sect. Melioideae), a tree yielding a moderately light timber, occurs sparingly in the Knysna region but is present in most of the other forests of the Union. At Knysna it occurs scattered in forest of medium-moist and dry types; occasional consociates are found near the coast. The species seems to be light-demanding (except in earliest youth) and to favour soils of moderate water-content. While the pH range is wide, the plant rarely occurs on soils of acidity greater than pH 4.9 at 9 to 12 inches.

No organisms live in symbiosis with it. The degree of fertilisation is low (1-5 per cent.): the seeds can lie dormant for a few months only: germination takes place within 2½-4 months of fall, the germinative capacity being 40-50 per cent.

- 73. van der Byl, P. A.** "Descriptions of some previously unnamed South African Fungi. III." *S. Afr. Journ. Sci.* **24**, pp. 225-226. 1927. (2. 29.)

New species of *Polyporus*, *Puccinia*, *Uredo* and *Fusicoccum* are described.

- 74. Phillips, J. F. V.** "Dendrographic Experiments: *Ocotea Bullata* E. Mey. (Stinkwood)." *S. Afr. Journ. Sci.* **24**, pp. 227-243, 4 text-figures. 1927. (2. 30.)

This is a preliminary account of dendrographic data collected for *Ocotea bullata* E. Mey. by means of MacDougal's instrument. Reversible variations were found to occur and the effect of habitat factors upon their range was found to be considerable. The occurrence of these reversible variations supports the view that light does not necessarily retard growth and shows that the influences of humidity, temperature, wind and rate of evaporation, coupled with soil-moisture, are of paramount significance to the living tree. It is held that extended investigation by means of the dendrograph would indicate which of various slope-exposures or soil-types would be likely to produce the least-effective drain upon the water-balance of a particular species. Various other applications of the method in elucidating problems in forest-ecology are suggested.

- 75. Fantham, H. B., Schuurman, Johanna F. M. and Robertson, Katherine G.** "Some Protozoa found in certain South African Soils. VII." *S. Afr. Journ. Sci.* **24**, pp. 346-376. 1927. (2. 31.)

This is a further contribution to the knowledge of the Protozoa of soils in southern Africa, soils from the Cape Province, Orange Free State, Transvaal, British Bechuanaland and Northern Zululand having been investigated. Seasonal variation has been studied in soils collected in Milner Park, Johannesburg.

- 76. Phillips, J. F. V.** "The Rôle of the 'Bush dove,' *Columba arquatrix* T. & K., in Fruit-dispersal in the Knysna Forests." *S. Afr. Journ. Sci.* **24**, pp. 435-440. 1927. (2. 32.)

The bush dove, *Columba arquatrix* T. & K., is briefly described and its habits of life outlined. The correlation of influx of bush doves and the full fruiting seasons of *Olea laurifolia* Lamk. is pointed out.

The time required for germination of a number of Knysna forest seeds is appreciably shortened by passage through the system of the bird.

The principal species dispersed by the bird are listed and it is concluded that the bush dove is more useful than harmful.

(3) AUSTRALIA (COLLABORATOR, V. S. SUMMERHAYES)

77. Cleland, J. B. and Black, J. M. "An Enumeration of the Vascular Plants of Kangaroo Island." *Trans. Roy. Soc. S. Austral.*, Adelaide, **51**, pp. 24-61. Dec. 23rd, 1927. (3. 6.)

78. Hamilton, A. G. "The Xerophytic Structure of the leaf in Australian Proteaceae. Part I." *Proc. Linn. Soc. New South Wales*, Sydney, **52**, pp. 258-274, 27 figures in the text. Oct. 25th, 1927. (3. 7.)

It is pointed out that the Proteaceae, in spite of their marked xerophytic characters, are not abundant in the dry central portions of Australia, but are frequent on wet sandy soil in the well-watered country nearer the coast. Descriptions of the anatomy of the leaves of 47 species of *Hakea* are given.

79. Cambage, R. H. "Acacia Seedlings. Part XII." *Journ. Roy. Soc. New South Wales*, Sydney, **60**, pp. 85-103, 4 plates. Oct. 29th, 1926. (3. 8.)

Among other information data is given of the vitality of seeds of *Acacia* spp. in the soil. Cases are cited of seeds germinating in ground recently ploughed where no trees had been present for periods of 35-68 years in different cases. In one locality over one thousand seedlings sprang up in a restricted area. During dry summers, when the ground cracks extensively, seeds fall into the cracks and remain dormant until ploughing brings them nearer the surface.

80. McLuckie, J. and Petrie, A. H. K. "The Vegetation of the Kosciusko Plateau. Part I. The Plant Communities." *Proc. Linn. Soc. New South Wales*, Sydney, **52**, pp. 187-221, 1 map, 9 plates, 8 figures in the text. Oct. 25th, 1927. (3. 9.)

The area studied lies in the south of New South Wales, being 20 miles long by 6 miles broad and lying between 3000 and 7000 ft. above sea-level. For six months of the year the higher portions are covered by snow. The underlying rock is gneissic granite. Three regions can be distinguished, viz. (1) the montane zone (3000-5000 ft.), (2) the sub-alpine zone (5000--tree line at 6000-6500 ft.), and (3) the alpine zone, lying entirely above the tree line.

The montane zone is mainly occupied by *Eucalyptus gunnii* forest, while the ridges and the slopes of the sub-alpine zone bear *Eucalyptus coriacea* forest. Accounts are given of the structure and adaptations of these forests including certain features of regeneration, while the factors affecting the tree-limit are discussed. Strong winds in winter are considered to be the most important factor, while the amount of summer rainfall is suggested as of significance.

The lower portions of the slopes of the sub-alpine region below the forest are covered with low-tussock grassland of *Poa caespitosa*, which together with mat-herb communities dominated by *Celmisia longifolia* occupies most of the alpine zone. In the valleys is a marsh vegetation consisting of reed-swamp in which different communities are dominated by *Hypolaena lateriflora* or *Restio australis*, and bush-swamp, the chief local dominants of which are *Richea gunnii*, *Epacris serpyllifolia*, *Baeckea gunniana* and *Callistemon sieberi*. The relationships between these various seral communities are discussed in detail.

81. Cunningham, G. H. "The Gasteromycetes of Australasia. Part IX. Keys to the Genera and Species of Lycoperdaceae." *Proc. Linn. Soc. New South Wales*, Sydney, **52**, pp. 247-257. Oct. 25th, 1927. (3. 10.)

An historical summary and short discussion of the genera are given.

- 82. McLuckie, J. and Petrie, A. H. K.** "An Ecological Study of the Flora of Mount Wilson. Part IV. Habitat Factors and Plant Response." *Proc. Linn. Soc. New South Wales*, Sydney, **52**, Pt 2, pp. 161-184, 20 text-figures. July 11th, 1927. (3. 11.)

This paper is a study of the habitat factors; and an attempt is made to correlate these with the distributional features of this region; and an explanation of (1) the small amount of invasion of the basalt by types from the *Eucalyptus* forests of the sandstone, (2) why the rain-forest grows as well in the sandstone gullies as in the sheltered basaltic slopes, is given.

The rainfall, temperature and evaporative powers of the atmosphere in the different habitats, the hydrogen-ion concentration of the soil-solution and the moisture content of the soil, are discussed in relation to their relative significance upon the distribution and organization of the various plant communities. The pH value of the soil solution is proved to be an insignificant factor in the distribution of the vegetation, while the moisture content of the soil is shown to be of greatest importance. The effect of aspect and moisture content outweighs that of all other factors. The responses of the more important components of the communities to the habitat factors are discussed, and the distribution of the communities is shown to be controlled by the water supply rather than by the geological formation.

The *Ceratopetalum-Doryphora* forest is the climax community upon the sheltered basaltic slopes and deep sandstone gorges, while the sub-mesophytic *Eucalyptus goniocalyx*-*E. blaxlandi* forest and the sclerophyllous *E. piperita*-*E. haemastoma* forest constitute the climax vegetation upon the more exposed habitats of the sandstone and basalt.—*J. McLuckie*.

- 83. Kessell, S. L.** "Soil Organisms—the dependence of certain pine species on a biological soil factor." *Empire Forestry Journal*, London, **6**, No. 1, pp. 70-74, 3 half-tone photographs. 1927. (3. 12.)

In connection with pine planting operations on a large scale in South Western Australia difficulties have been experienced in raising seedlings in new nurseries. This is a region practically devoid of natural *Coniferae*, and all species dealt with have been exotic. The species used mainly in the plantations have been *Pinus insignis* and *P. pinaster*, although many other species planted on an experimental scale, including *P. canariensis*, *P. muricata*, *P. taeda*, *P. caribaea* and *P. halepensis*, have behaved similarly.

Germination in new nurseries, whether established on virgin land or old cultivations was found to be satisfactory, but plants failed to develop after the first month or two, and assumed an unhealthy colour. By tests extending over several years factors such as soil moisture, fertility, acidity, and disease were eliminated as possible explanations. In all nurseries a very small percentage of healthy seedlings occurring in small patches was noticed. These patches could not be associated with any physical or chemical condition of the soil, but the roots of healthy seedlings were noticed to have:

- (a) Fungal mycelium in close association (by macroscopic examination).
- (b) Swollen root hairs which divide and show a coralline formation.

The survival of seedlings after transplanting from nursery beds to plantation areas was found to have a direct relation to the extent of fungal association in the nursery.

Numerous field tests indicated that the required soil factor is an exotrophic mycorrhiza. Both in "well infected" nurseries and in plantations which have been successfully established, many fruiting bodies of *Rhizopogon roseolus* have been found at certain seasons.

A new nursery site can be made to produce first-class planting stock by applying a dressing of soil from an old-established pine nursery. The obligatory association of the young pine with soil organisms is now accepted in connection with all pine planting operations carried out by the Western Australian Forests Department.—*S. L. Kessell*.

(4) NEW ZEALAND (COLLABORATOR, V. S. SUMMERHAYES)

- 84. Cockayne, L. and Allan, H. H.** "The Bearing of Ecological Studies in New Zealand on Botanical Taxonomic Conceptions and Procedure." *Journ. Ecol.*, Camb. Univ. Press, **15**, pp. 234-277. Aug. 1927. (4. 12.)

The authors draw attention to the lax use of the word "species" in taxonomy, and discuss the various definitions which have been proposed by different writers. They also point out the loose application of the term "variability" and suggest in its place "polymorphy" which is then defined and illustrated with examples of New Zealand plants. Different types of polymorphy are distinguished, including that occurring in the individual, that occurring in groups of related individuals, and finally heteroblastism. In each examples are cited.

Following this the authors deal with terminology, recognising the jordanon and the species, this latter being simple or compound according to whether it contains one or more jordanons. Unstable habitat forms are termed "epharmones."

Methods of collecting, labelling, etc., in the field are then given, stress being placed on care and fullness of observation and notes. New suggestions for the arrangement of herbaria are put forward and the value of the experimental garden is emphasised.

A detailed account of the various taxonomic units follows, these being illustrated by many examples from the New Zealand flora. Especially is the term epharmones dealt with very fully. The great resemblance between epharmones of one species and "normal" plants of another is pointed out and the need for accurate study stressed. Finally the question of hybrids is discussed at length, many examples being cited, and systems of nomenclature for such briefly touched upon.

Throughout the paper the importance of ecological work in the field is urged, and the conviction expressed that much is required to be done along these lines.

- 85. Laing, R. M.** "The External Distribution of the New Zealand Marine Algae and Notes on some Algological Problems." *Trans. New Zealand Institute*, Wellington, **58**, pp. 189-201. Oct. 18th, 1927. (4. 13.)

The phytogeographical relationships of the various groups are discussed, special attention being paid to the Phaeophyceae. These are shown to be mainly Australasian in their affinities.

- 86. Smith, J. Crosby.** "The Vegetation of Awarua Plain." *Trans. New Zealand Institute*, Wellington, **58**, pp. 55-56, 1 half-tone plate. Aug. 4th, 1927. (4. 14.)

Awarua Plain is a large swampy bog in Southland Province, which is occupied largely by sub-alpine plants characteristic of higher latitudes. Drainage is now killing off much of the original vegetation. *Sphagnum* spp., *Donatia novae-zealandiae*, *Phormium tenax*, *Leptospermum scoparium* and *Danthonia raoulii* var. *rubra* dominate in different areas according to the amount of drying out, the last named occupying the driest portions.

- 87. MacKenzie, J. G. and Cockayne, L.** "The Otari Open-air Native-Plant Museum." *N.Z. Journ. Agric.* **34**, pp. 309-321, 9 figures (half-tone from photos). Wellington, May 20th, 1927. (4. 15.)

In this article is told how Wilton's Bush, or the Otari Native-Plant Museum, came into the hands of the Government, which constituted it a scenic reserve, and how, later, it was acquired by the Wellington City Council, partly by purchase. Further, it is explained how the purpose of the reserve was altered—largely through the action of the New Zealand

Institute of Horticulture—and how it has been constituted an “open-air native-plant museum” where nothing is to be grown save the indigenous plants of the New Zealand region.

The plan upon which the museum is to be arranged—a plan approved by the City Council—is explained at some length. Briefly, it consists of a fourfold scheme, including (1) a collection of all the New Zealand species which can be grown; (2) examples, to be artificially made, of various important features of the primeval vegetation of New Zealand—this a unique undertaking; (3) the use of indigenous plants for horticultural purposes to be illustrated in various ways for the information of those desirous of using such plants in their gardens; and (4) the restoration of the present forest to what it was originally.

This plan in its entirety is the first to be formulated in any part of the world. As the flora and vegetation of New Zealand are considered of special interest the world over, the future development of the Otari Open-air Native-Plant Museum will be followed closely by all students of botany.—*L. Cockayne.*

- 88. Cockayne, L.** *New Zealand Plants and Their Story*. Third edition, revised throughout, pp. xvi + 271, illustrated with 99 photographs and 11 drawings. New Zealand Board of Science and Art, Manual No. 6. W. G. Skinner, Government Printer, Wellington, New Zealand, 1927. Price, cloth 10s. 6d., paper back 7s. (4. 16.)

The third edition of a well-known popular book dealing with the vegetation of the New Zealand Botanical Region and giving much ecological information regarding a large proportion of the species. This edition appears in a new guise, the figures being arranged amongst the text and all printed on art paper. Though somewhat shorter than edition 2, only a certain amount of rather technical matter is excluded. The genus *Hebe* is substituted for the shrubs and trees previously referred to *Veronica*; there is a good deal regarding wild hybrid swarms—at present, the most important development of New Zealand botany—and, in the Index to each Latin name the popular name—if there be such—is appended in brackets, as is the Latin name to each popular name. The account of the vegetation is brought up to date and so, too, the nomenclature of the species.—*L. Cockayne.*

- 89. Cunningham, G. H.** “The Polyporaceae of New Zealand.” *Trans. New Zealand Institute*, Wellington, **58**, pp. 202–250, 11 plates. Oct. 18th, 1927. (4. 17.)

Descriptions of all the species are given together with keys to the genera and species.

- 90. Wilson, J. H.** “Some crevice plants from the lava field at Mount Wellington.” *Trans. New Zealand Institute*, Wellington, **58**, pp. 255–263, 2 plates, 3 figures in the text. Nov. 8th, 1927. (4. 18.)

The crevice plants are chiefly developed on the southern side of the lava seams. The soil held in the crevices is of fine texture and contains much humus. Readings showed that the relative humidity inside the crevices is greater than outside. *Astelia solandri* is the commonest species, followed by *Peperomia urvilleana*, while the ferns *Polypodium billardieri*, *Pellaea rotundifolia* and *Asplenium flabellifolium* are also abundant. An account of the morphology and anatomy of certain organs of the above-mentioned species is given and these are related to the habitat. The structure of *Astelia* shows various features which suggest explanations for its dominance in this specialised community.

(5) PACIFIC ISLANDS (COLLABORATOR, V. S. SUMMERHAYES)

91. **Christophersen, Erling.** "Vegetation of Pacific Equatorial Islands." *Bernice P. Bishop Mus. Honolulu, Bull.* **44**, pp. 1-79, 7 plates, 13 figures in the text. 1927. (5. 4.)

The paper describes the climate, soils and types of vegetation of seven coral islands of the Central Pacific Ocean near the equator: Palmyra, Washington, Fanning, Christmas, Jarvis, Baker and Howland. The three first-named islands are located in a belt of abundant precipitation, while Christmas Island lies in a transition region to a dry belt in which the last-named islands are located. The normal rainfall on Fanning Island (14 years) is 2733.2 mm. (107.60 in.), comparable to that of the lower part of the rain-forest of high islands. The temperature is very similar on all islands and extremely uniform throughout the year. On Fanning Island the mean monthly temp. (12-15 years) is 26.5° C. (80° F.) for all months except January with 26° C. (79° F.). Evaporation in the open is very high on all islands. On Christmas Island the average for three atmometers during 72 hours is 41 c.c. (corrected reading) per 24 hours, indicating a semiarid climate.

The soils are prevailingly sandy, of a distinct alkaline reaction (average pH about 8), and with little humus admixture. In places, however, they are phosphatic molds with an acid reaction of pH 5-6, or peaty, in which case the H-ion concentration may be still higher. Nine soil profiles are illustrated. On Washington Island the lagoon has been cut off from the sea and converted into a freshwater lake and a peat bog, unique features for coral islands, or tropical lowlands as a whole. The peat is similar to that formed in temperate regions, showing the structures of the plants that made it. It averages about 7 ft. deep above the coral sand bottom. The acidity is pH 5.9-6.0 in the surface layer.

On the islands in the wet belt the principal vegetation type is the coconut forest, in places in a semi-natural state. Other forests are dominated by *Pisonia grandis*, especially on phosphatic soils, *Pandanus tectorius* (and spp.) in wetter localities, and *Tournefortia argentea* on the beach crest. Ferns, especially *Polypodium scolopendrium*, are common in the bottom layer of the forests. The principal scrub type is the *Lepturus repens*-*Sida fallax* scrub, present on most of the islands and particularly prominent on Christmas Island. *Scaevola frutescens* also forms open or closed scrubs. On Christmas and Fanning Islands the dwarf shrub *Heliotropium anomalum* is prominent. In the bog of Washington Island *Scirpus riparius* is the most important species. In open unprotected localities, especially the beach crest, the bunch grass *Lepturus repens* is prominent on all the islands. On the islands of the dry belt no forests are present (with the exception of a grove of *Cordia subcordata* on Howland Island), and the vegetation is mainly made up of *Lepturus repens* on the beach crest, and *Portulaca lutea* and *Boerhaavia tetrandra* in the interior.

The vascular flora of the islands is known to consist of a total of 60 species divided among 48 genera, the generic coefficient having the very high value of 80, an indicator both of the young age of the islands and of obstructed immigration. Most of the species are of widespread occurrence. About 39 species may be considered to be native, while 20 species have been accidentally introduced by man, and one species has run wild from cultivation. *E. Christophersen.*

(8) TROPICAL AND NORTH AFRICA (COLLABORATOR, T. F. CHIFF)

92. **Lavauden, H.** *Les Forêts du Sahara.* Pp. 26, plates 5. Paris: Berger-Levrault, 1927. Price 2 fr. 50. (8. 1.)

The author justifies his use of the title by stating that for the greater part it refers to the forests that no longer exist but of whose former extent ample evidence abounds. To-day, however, the term may actually be applied to numerous localities in the Sahara.

The phytogeographical limits and the principal aspects of the Sahara are discussed in connection with Dr René Maire's division of the "région saharienne" into three "domaines": "le domaine saharien septentrional," "central" and "méridional." Areas where life is totally absent such as the celebrated Tanezrouft to the south of Hoggar, the Hammada of Tingher, the Ténéré in the eastern Sahara, form only a small part. The concept of these "domaines" and their sub-divisions as given by different writers is examined in the light of the author's own experience.

The general characters of the Sahara vegetation are mentioned and the former and present extent of wooded areas are indicated. Twenty-nine woody species are enumerated with notes of their distribution. A specimen of the Tarout (*Cupressus Dupreziana* A. Camus), of which a photograph is given, existing in the mountains of Tassili des Azdgers, between Rhât and Djanet is considered to be about a thousand years old and the sole remnant of a former forest. Its seeds are now infertile.

The concluding section deals with the climatic problem. Evidence is quoted in support of the continued desiccation of the Sahara. The author considers that protection from pasturage and fires may win back the vegetation in some parts, but is of the opinion that the greatest hope of rendering some areas fertile is by the construction of barrages at suitable points.

93. Verdoorn, I. C. "Revision of the African Toddalieceae." *Kew Bull.* 9, pp. 389-416. 1926. (8. 2.)

The paper considers the evolutionary tendencies of the *Rutaceae* in general, and points out the primitive characters in contrast to the more advanced ones, with special reference to the *Toddalieceae*. The genera of this group number seven, and, with the exception of *Toddalia* and *Vepris*, they are confined to Africa and the Mascarene Islands. Distribution maps are given of the more widely occurring genera and it is noted that these genera show the more advanced characters. A diagram shows the phylogenetic relationship of the genera under review. The group is an extremely homogeneous one, and presents considerable difficulty in the separation of genera and species. In framing the generic key the relative number of stamens and petals, in conjunction with the number of ovary cells, has been mainly relied upon. Specific distinction depends chiefly on inflorescence and leaf characters, together with the relative evidence of gland-dots, and indumentum. Several new combinations and new species have been made.—*M. B. Moss.*

94. Snowden, J. D. "Notes on African Grasses. VII." *Bulletin of Miscellaneous Information*, Royal Botanic Gardens, Kew. 1928, No. 4. Pp. 130-132. (8. 3.)

Three grasses are enumerated from the slopes of Mt Elgon in Uganda, and the opportunity is taken of publishing some extracts from Mr Snowden's field notes on the vegetation of the area. Three main grazing lands for stock are differentiated. One covered with tall, strong-growing grasses occurs at altitudes from 3500 to 5000 ft. (or up to 6000 ft. in drier localities), and is natural savannah or cultivated land which has been abandoned for a long time. Within the same altitudes occurs land recently under cultivation but now abandoned. This is covered by shorter and weaker grasses which form a short, open turf, liable to dry out and be destroyed in the dry season by white ants. In wet localities from 5000 to 8000 ft. grasses occur only in clearings in the natural bush and forest. Following on cultivation, however, many other grass invaders appear and form a thick matted turf eagerly sought after by stock. *Oxytenanthera abyssinica* Munro is one of the grasses enumerated and Mr Snowden remarks that this species at present covers many square miles in the Simu Valley, but formerly it extended over greater areas.

95. **Duke, M. M.** "Fungi from Kenya Colony." *Kew Bull.* 8, pp. 305-320. 1926. (8. 4.)

A systematic enumeration is made of the fungus flora of Kenya Colony, the material received at Kew having been sent by various collectors.—*M. B. Moss.*

96. **Hutchinson, J. and Danby, J. E.** "A new Genus from Uganda." *Kew Bull.* 8, pp. 363-365. 1926. (8. 5.)

A new genus of *Polygonaceae* is described, *Harpagocarpus*, whose nearest affinities are the genera *Polygonum* and *Fagopyrum*, from which it can readily be distinguished by the large fruit armed with barbed setae. The setae are emergences from the ovary wall and do not correspond to any feature in the rest of the *Polygonaceae*. A single species, *H. Snowdenii* Hutch. et Dandy, sp. nov. is described from a specimen collected by Mr J. D. Snowden on Mt Elgon; the description is accompanied by a figure in the text.—*M. B. Moss.*

97. *East African Pasture Plants. I. East African Grasses.* The Crown Agents for the Colonies, 4 Millbank, London, S.W. 1926. Pp. 56, text-figs. 28. Price 2s. 6d. (8. 6.)

The book, which has been prepared at Kew, contains descriptions and illustrations of twenty common East African grasses. In the introduction a typical grass plant is simply described and details of the floral structure are given with illustrations of the essential parts. There is also a simple account of the general principles on which the classification of grasses is based. The description of each species is accompanied by a text-figure, together with notes on the vernacular names, distribution, habitat, and economic uses. The object of the work is to assist agricultural workers in determining the more common grasses in the field.—*M. B. Moss.*

98. *East African Pasture Plants. II. East African Grasses.* Pp. 55 with 26 full-page illustrations. Crown Agents for the Colonies, 4 Millbank, London, S.W. 1927. Price 3s. (8. 7.)

Part I of the *East African Pasture Plants* dealt with a number of species specially selected to illustrate the various groups of families; the present contribution deals more particularly with the common pasture grasses of Kenya Colony, Uganda and Tanganyika Territory, with the view to making their identification more easy to the agriculturist. Twenty-six species have been selected and described in simple language, each being accompanied by a full-page drawing illustrating the habit and magnified dissections of the flower.—*M. B. Moss.*

99. **Blunt, H. S.** *Gum Arabic; with special reference to its Production in the Sudan.* Pp. 47, map, ill. 50. Oxford University Press, London: Humphrey Milford. 1926. Price 10s. 6d. net. (8. 8.)

The work is entirely devoted to Gum Arabic or Gum Senegal (*Acacia Senegal* Willd.; *A. Vereh* Guill. & Perr.), and establishes the importance of the main trade product of an extensive tract of the Sudan region. About two-thirds of the gum exported from the Sudan comes from the Kordofan Province which covers some 119,000 square miles. Throughout the Province the Forestry Staff exercise control, distributing seed, encouraging cultivation, preventing illicit cutting down of trees and supervising the markets. The best gum areas are reported to be in comparatively dry regions. The gum trees are found to be best grown from seed, which is produced only about once in every five years, and the production of gum is estimated to lie between the fourth and eighteenth years.

In general the book deals with the History of the Trade, the Kordofan Province, Exploitation, Markets, Forest Policy, Chemical Properties and Uses of the Gum. The illustrations are an important feature of the work.—*M. B. Moss.*

- 100. Wilson, R. C. and Bain, A. D. N.** "The Nigerian Coalfield." *Geological Survey of Nigeria*, Bulletin No. 12, 6 plates and a coloured geological map. With an appendix by SPATH, L. F., on "The Albian Ammonoidea of Nigeria," pp. 54. 1928. (8. 9.)

The geological investigations of the area described were carried out by Dr Wilson in 1926, and by Dr Wilson and Mr Bain in 1927. An outline map of Nigeria is given showing the position of the region surveyed, which lies between the $5^{\circ} 30'$ and $6^{\circ} 15'$ lines of latitude, and stretches from west to east from longitude $6^{\circ} 45'$ to $7^{\circ} 30'$. It forms an area of about 2650 sq. miles, and lies wholly within the political provinces of Onitsha and Owerri.

The geological formations represented in the area are: Recent, Tertiary, Upper and Lower Cretaceous. A general account is given of the geological structure and history, followed by a more detailed description of the lithology of the different systems. A section is devoted to Physiography, giving a description of the topography and drainage. The physical features are intimately related to the geology and are dependent on the relative resistance to erosion of the underlying rocks. Roughly the country can be divided into two areas:

1. Level sandy plains to the south.
2. Dissected belt of country rising northwards.

The latter forms a stretch of gently undulating slopes with a luxuriant covering of bush and scrub; dark clumps of big trees indicate the site of native villages. The area is much under cultivation, as the native population is large.

A series of plates, accompanied by descriptions, gives the principal features in graphic form.—*M. B. Moss.*

- 101. Good, R. d'O.** "Notes on Captain G. N. Humphrey's Plants from the Ruwenzori Mountains." *Journ. Bot.* **66**, pp. 37-41. Feb. 1928. (8. 10.)

The expedition in 1926 under Captain G. N. Humphreys crossed the largest hitherto unexplored area in the Ruwenzori Range, an area shown on recent maps as "inaccessible country covered with dense forest." The centre of the region consists of a treeless plateau on which the only flowering plants are two species of *Alchemilla*. The major part of the collection of plants was made in the highest floral zone, which extends from about 12,800 ft. to the snow-line at about 14,800 ft. A fairly extensive collection was also made in the second highest zone, from 12,000 ft. to about 12,800 ft., and an enumeration of the plants of the two belts occurs. The species in the two zones are different but it was found that for some distance on each side of the dividing line there is considerable overlap.

The collection contains three species not already described: *Thunbergianthus ruwenzoriensis* R. Good, and the new form *macrocalyx*; *Senecio Humphreysii* R. Good; *Deschampsia angusta* Stapf et Hubbard.—*M. B. Moss.*

- 102. Borg, John.** *Descriptive Flora of the Maltese Islands including the Ferns and Flowering Plants.* Pp. 846. Government Printing Office, Malta. 1927. 5s. (8. 11.)

This is the first full descriptive flora of the Maltese Islands to be published and appears to have been carefully compiled. Essentially it is taxonomic with concise descriptions of the families, genera, species, and varieties so far recorded from Malta and its sister islands. Detailed localities are quoted for all the rarer plants and habitat notes, general distribution,

flowering periods, vernacular names, and uses are also given. An interesting introduction deals with the botanical history of Malta, the geology, water supply, climate in reference to vegetation, and, briefly, with the ecology and phytogeography. There are no illustrations or keys.—W. B. Turrill.

- 103. Humphreys, G. N.** "New Routes on Ruwenzori." *Geographical Journal*, London, 69, No. 6, pp. 516-531, plates 10. June, 1927. (8. 12.)

The Ruwenzori Range was entered from the east, the expedition explored Mt Stanley and Mt Speke on the west side and descended from the north-west slopes. Plants typical of the chief zones of vegetation are recorded. After passing through the difficult bamboo zone, through which a track had been prepared, they reached what is described as the most beautiful and interesting floral zone where were species of *Ranunculus*, *Cardamine*, *Viola*, *Orchis*, *Rubus*, *Hypericum*, docks and nettles. The vegetation of the highest floral zone of the mountains at about 14,000 ft. altitude is characterised by a species of *Senecio*—the Omukoni tree—herbaceous *Lobelias* about 15 ft. high, a *Galium*, an *Arabis*, and Umbellifer and shrubby everlastings. The general conditions at this altitude are constant mists, rain and snow-storms.

- 104. Hutchinson, J. and Dalziel, J. M.** *Flora of West Tropical Africa*, 1, Pt I, pp. i-x, 1-246, text-figs. 108, map 1. The Crown Agents for the Colonies, 4 Millbank, London, S.W. 1927. Price 8s. 6d. (8. 13.)

This is the first of the regional Floras within the area covered by the "Flora of Tropical Africa" to be prepared at the Royal Botanic Gardens, Kew. Introductory Chapters deal with Botanical Exploration in West Africa, a Bibliography of Works dealing mainly with the Botany of West Africa, a Glossary of Botanical Terms, a Key to the Principal Groups of Plants as arranged in the Flora, and Artificial Keys to the Families of Dicotyledons and Monocotyledons represented in the Flora. The Enumeration begins with the Cyadaceae and covers the Families Anonaceae to Tiliaceae according to Hutchinson's system of Classification; descriptions of species are confined to the keys. The object of this Flora is to include all phanerogams recorded within the area bounded on the north by the Tropic of Cancer and on the east approximately by the 15° E.

- 105. Chipp, T. F.** *The Gold Coast Forest: a study in synecology*. Pp. 34, plates 7, text-figs. and maps 30. *Oxford Forestry Memoirs*, Number 7, 1927. Clarendon Press, Oxford. Price 10s. (8. 14.)

The first part of this work is devoted to a discussion of the local habitat factors. The general features of the country are reviewed and the activities of the native population in its relation to the forest. A general description of the forest is given and its connection with the vegetation of West Africa is described. The climatic factors are discussed in detail and it is to their influence that the author attributes the differentiation of the forest types. Short chapters on soil and biotic factors close the first part.

In the second part the types of forest vegetation are enumerated and described in the light of the information given in the first part. The forest is considered as a whole comprising one Association and three Preclimaxes differentiated by the south-west Monsoon in its waning influence from the point of incidence at the south-west corner of the country towards the hinterland. The general lines of Succession of the forest types are indicated and the most striking seral units described. A chapter is devoted to a description of the country surrounding the forest and the interaction of forest and parkland is discussed. Maritime vegetation is treated separately as edaphic climax units. The general scheme of the work is based on the system of F. E. Clements as modified in *Aims and Methods in the Study of Vegetation*. Two final chapters indicate the many interesting problems awaiting intensive

study which are now able to be followed up owing to the elucidation of the general problems, which have been provided in Parts I and II. These problems concern the study of plant forms, especially the suggested ecads of the species represented in forest and parkland, or in different types of forest. Attention is also drawn to the value of Indicator species and communities, and several examples are quoted.

The work is fully illustrated by text-maps showing the forest areas and operation of climatic factors and diagrams and charts of the distribution of vegetation types and the general lines of Succession. The combined climatic charts provide graphic explanations, easy of comparison, of the climates prevailing in different typical localities within and without the forest, and from them the author has deduced an "ideal climatic chart" for the optimum of the forest. This is the first synecological study of the Gold Coast forest and the general principles employed in this investigation are applicable generally to other areas of the Tropical African forest.

(9) CENTRAL AND SOUTH AMERICA (COLLABORATOR, R. C. McLEAN)

106. Johnson, Duncan S. "Re-vegetation of a Denuded Tropical Valley."

Botanical Gazette, **84**, pp. 294-306, 5 figs. 1927. (9. 1.)

The Cascade Valley in the Blue Mountains of Jamaica lies in a typical montane forest region and before November, 1909, it bore forest continuous with that on neighbouring slopes. On the 8th and 9th of that month it received 27 in. of rain and it was entirely denuded of vegetation by the resulting flood. Everything was cleared off and the surface reduced to a waste of boulders and gravel. The author has paid three subsequent visits to the valley and describes the process of recovery up to July, 1926. The observations are to be continued.

In 1910 the only plants visible were seedlings of a few common dicotyledons, chiefly *Bocconia frutescens*.

In 1919 the most abundant plant was *Gloeocapsa magma*, forming velvety crusts on the bare rock-surfaces. This was accompanied by 7 ferns, 1 monocotyledon and 22 dicotyledons, of which nearly half were Compositae and more than half were woody. The dominant species was *Vernonia permollis*.

In 1926, 20 thallophytes and 58 cormophytes were established. The dominance had passed to *Baccharis scoparia* and *Dodonaea angustifolia* which had sprung, since 1919, from insignificance to the stature of 8 ft. bushes occurring by hundreds. These plants are only now beginning to produce a scanty humus, so that one is astonished to hear of *Psilotum nudum* and *Bletia verecunda* (Orchidaceae) growing freely among the loose stones. One sterile moss alone represented the Bryophyta; lichens were very sparse.

In two important respects these observations show a course of events the reverse of that supposed to be usual in re-vegetation. The first is the slowness with which the process has gone on, in a moist, hot climate. Nearly ten years after denudation nine-tenths of the area was still bare. The second is the sequence of succession. The primary colonists were (with the exception of *Gloeocapsa* on the rock-surfaces) all woody dicotyledons. Herbaceous angiosperms and ferns appeared only secondarily; while lichens and bryophytes have scarcely yet arrived, even sixteen years after the flood.

107. Alston, R. A. "An Examination of the Potaro-Ireng District." *Report of the Department of Science and Agriculture, British Guiana*, 1926. Georgetown, Demerara, 1928. (9. 2.)

This is a forest region bounded by the Kopinang, Arnik and Tumong rivers. It stands upon a deep friable soil, derived from the underlying gabbro and suggesting agricultural possibilities.

The dominant trees are Leguminosae, the Atuba (*Dicymbe* sp.) and the Sand-mora (near *Dimorphandra*), which occur in almost pure stands. Beyond the Essequibo-Ireng watershed occur savannahs at a height of 2500-3000 ft. Where these border the forest there are thickets of tall *Panicum magnum*.

The savannah soil is a thin sand overlying conglomerate and sandstone beds and is covered with wiry tufts of sedges and grasses, with interspersed herbs and small, isolated *Psidium* trees.

Woodland "oases" in depressions and along the river channels give the country a park-like appearance.

The transition from forest to savannah appears to be governed principally by precipitation, the trade-winds depositing most of their moisture on the N.E. slopes of the Pakaraima Mountains, where forest is to be found at the same altitude and on the same soil as the savannahs on the other side of the watershed.

108. Leonard, E. C. "*Ruellia tuberosa* and a few of its close relatives." *Journal of the Washington Academy of Science*, **17**, pp. 509-520. 1927. (9. 3.)

109. Standley, P. C. "New Plants from Central America." *Journ. Wash. Acad. Sci.* **17**, pp. 520-528. 1927. (9. 4.)

110. Gleason, H. A. "Studies on the Flora of Northern South America." *Bulletin Torrey Bot. Club*, **54**, pp. 603-618. 1927. (9. 5.)

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